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The Production Biology of the Lower Laurentian Great Lakes — A Preamble

RICHARD A. VOLLENWEIDER

Department of the Environment, Fisheries and Marine Service
Great Lakes Biolimnology Laboratory
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

THE majority of papers collected in the following section are the results of an initial study on the production biology of lakes Ontario and Erie. A few papers related to this study have been published, or are in press elsewhere, i.e. Lake Ontario phytoplankton (Munawar and Nauwerck 1971); The seasonal cycle of pheopigments in Lake Ontario with particular emphasis on the role of zooplankton grazing (Glooschenko et al. 1972); Surface distribution of total chlorophyll *a* in lakes Ontario and Erie, 1970 (Glooschenko et al. 1973); and Chlorophyll *a* distribution in Lake Huron, its relationship to primary production (Glooschenko et al. 1974). Vollenweider et al. (1974) have given a review of phytoplankton and primary production in the Laurentian Great Lakes.

These studies have been conducted by the Fisheries Research Board Detachment located at the Canada Centre for Inland Waters, Burlington, Ont., as part of the limnological programs of the Eutrophication Section of the Freshwater Institute, Winnipeg, Man.

History and motivation of these programs, in the context of other programs of the above institute, have been summarized by Johnson and Vallentyne (1971). The FRB studies on the Great Lakes, from the fall of 1968 on, have been my responsibility, but were also closely related to studies carried out by the Lakes Research Division of the Inland Waters Branch (Department of Energy, Mines and Resources, now Department of the Environment). Because of the rapidly changing development taking place at the Canada Centre for Inland Waters (CCIW), and my promotion to Chief, Lakes Research Division, the above program was then continued first by Dr A. Nauwerck, and later by Dr W. Glooschenko.

The particular philosophy of the biological program grew out of several considerations. First, a literature review revealed that little was known on lakewide productivity of the Great Lakes. Previous studies on productivity were either confined to a few local areas, or, in cases of whole-lake surveys, restricted to one or two cruises per year, hence giving practically no information on temporal variations.

At that time, the Lakes Research Division at CCIW was already involved in an extensive chemical, physical, and sedimentological monitoring program (as part of its commitment to the study program of the International Joint Commission) to assess the state of pollution and eutrophication of lakes Ontario and Erie. The field studies of this program covered a station net of some 50–100 stations per lake (see Anon 1969). Only a small biological survey program was connected with the above studies

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(see Anon 1969; Patalas 1969; and Nicholson 1970).

The resources available to the FRB Detachment did not allow it to conduct a correspondingly extensive program on biological factors. Thus, the question then arose whether to attempt a similar though reduced field program, or to concentrate efforts on an in-depth study at a few stations. With the former approach, one would have had to sacrifice any information on processes along the vertical axis of the lake; with the latter, the spatial variability could not be investigated adequately.

In considering the scarcity of information on spatial and temporal variations, and the need to pinpoint areas of concern, the decision was made to initiate a program on as many stations as possible, i.e. about 35 stations in Lake Ontario, and 25 in Lake Erie, including in the study distribution of chlorophyll, phyto- and zooplankton, dry weight, etc., and measurements on board ship of primary production, supplemented by a few in situ expositions. Further, a reduced program on nutrients (phosphorus, nitrogen, silica) and trace elements was also added.

In view of the results achieved with a very limited manpower resource, the decision was probably the right one. Though the spatial and temporal resolution obtained is not entirely satisfactory, the outcome of the study has shown a number of essential features of the production dynamics in both lakes Ontario and Erie, and also has given a first insight into the degree of coupling or uncoupling of the biological processes with chemical and physical factors.

The results of these studies have been elaborated by several participants in this program but W. Glooschenko played an important role in assembling the different components, as seen from the many papers in which he appears as the principal author. Thanks are given to him, as well as to all other participants for their continuing input.

I wish further to thank the Director of CCIW, J. P. Bruce, for his continuing support, as well as the staff of the Water Quality Laboratories for their participation in the chemical–analytical programs, in particular V. Chawla. W. Johnson and J. Vallentyne from the Freshwater Institute, Winnipeg, assisted in numerous ways during the entire study period, and provided the essential financial support required for the development of the Detachment.

ANON. 1969. Pollution of Lake Erie, Lake Ontario, and the International Section of the St. Lawrence River. Report to the International Joint Commission by the International Lake Erie Water Pollution Board, and the International Lake Ontario–St. Lawrence River Water Pollution Board. Vol. 1–3.

GLOOSCHENKO, W. A., J. E. MOORE, AND R. A. VOLLENWEIDER. 1972. The seasonal cycle of pheopigments in Lake Ontario with particular emphasis on the role of zooplankton grazing. Limnol. Oceanogr. 17: 597–605.

1974. Chlorophyll *a* distribution in Lake Huron and its relationship to primary production. Proc. 16th Conf. Great Lakes Res. 1973, Int. Assoc. Great Lakes Res. (In press)

GLOOSCHENKO, W. A., H. F. NICHOLSON, AND J. E. MOORE. 1973. Surface distribution of total chlorophyll *a* in Lakes Ontario and Erie, 1970. Fish. Res. Board Can. Tech. Rep. 351: 25 p.

JOHNSON, W. E., AND J. R. VALLENTYNE. 1971. Rationale, background, and development of experimental lake studies in northwestern Ontario. J. Fish. Res. Board Can. 28: 123–128.

MUNAWAR, M., AND A. NAUWERCK. 1971. The composition and horizontal distribution of phytoplankton in Lake Ontario during the year 1970. Proc. 14th Conf. Great Lakes Res. 1971, Int. Assoc. Great Lakes Res. 69–78.

NICHOLSON, H. F. 1970. The chlorophyll *a* content of surface waters of Lake Ontario, June to November, 1967. Fish Res. Board Can. Tech. Rep. No. 186: 32 p.

PATALAS, K. 1969. Composition and horizontal distribution of crustacean plankton in Lake Ontario. J. Fish. Res. Board Can. 26: 2135–2164.

VOLLENWEIDER, R. A., M. MUNAWAR, AND P. STADELMANN. 1974. A comparative review of phytoplankton and primary production tn the Laurentian Great Lakes. J. Fish. Res. Board Can. 31: (In Press)

Primary Production in Lakes Ontario and Erie: A Comparative Study

WALTER A. GLOOSCHENKO, JAMES E. MOORE, MOHIUDDIN MUNAWAR,
AND R. A. VOLLENWEIDER

Department of the Environment, Fisheries and Marine Service
Great Lakes Biolimnology Laboratory
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

GLOOSCHENKO, W. A., J. E. MOORE, M. MUNAWAR, AND R. A. VOLLENWEIDER. 1974. Primary production in lakes Ontario and Erie: a comparative study. J. Fish. Res. Board Can. 31: 253–263.

Primary production values in Lake Ontario were low in winter, reached a maximum in midspring, declined during summer, and slightly increased in fall. Rate of increase of production for inshore waters (<20 m depth) was greater especially in spring and early summer with a greater maximum reached earlier than in offshore waters. Assimilation numbers, mgC fixed/mg chlorophyll *a* per hour, in Lake Ontario were fairly constant over the lake with a yearly range of 1.2–1.6. Primary production showed a linear relationship to chlorophyll *a* concentration, as also occurred in Lake Erie.

Lake Erie primary production varied in its three basins. Seasonally, in the Eastern Basin, production was highest in spring with a midsummer decline, and small peaks in fall. The Western Basin had a maximum in midsummer whereas the Central Basin had peaks in late summer and early fall. Assimilation numbers were highest in the Western Basin (up to 3.5 mgC/mg chlorophyll *a* per hour) and lowest in the mid-Central Basin and Eastern Basin with values of approximately 1.4 mgC/mg chlorophyll *a* per hour. A definite westerly increase of assimilation number was observed.

Up to early summer, the two lakes were fairly equal in surface production but integral photosynthesis, mgC/m^2 per hour was higher in Lake Ontario than in Lake Erie. The same was valid in November and December. In summer, Lake Erie was higher in production on both a mgC/m^3 per hour and mgC/m^2 per hour basis. For the period, April–December, Lake Ontario's total estimated yield was 170 gC/m^2, whereas for Lake Erie values of 160, 210, and 310 gC/m^2 were found for the Eastern, Central, and Western basins, respectively.

GLOOSCHENKO, W. A., J. E. MOORE, M. MUNAWAR, AND R. A. VOLLENWEIDER. 1974. Primary production in lakes Ontario and Erie: a comparative study. J. Fish. Res. Board Can. 31: 253–263.

La production primaire du lac Ontario est faible en hiver, atteint un maximum au milieu du printemps, diminue en été et augmente légèrement en automne. Le taux d'augmentation de la production dans les eaux du littoral (< 20 m de profondeur) est plus grand, surtout au printemps et au début de l'été, et atteint un maximum plus élevé plus tôt dans la saison que celui des eaux du large. L'indice d'assimilation, mgC fixé chlorophylle *a*/h, dans le lac Ontario est assez uniforme dans tout le lac, avec gamme annuelle de 1.2–1.6. La production primaire montre une relation linéaire avec la teneur en chlorophylle *a*, ce qui est également le cas dans le lac Erié.

La production primaire du lac Erié diffère dans ses trois bassins. La production du bassin de l'est est maximale au printemps, décline à la mi-été et montre des petits sommets en automne. Le bassin de l'ouest accuse un maximum à la mi-été, alors que dans le bassin central, il se produit des sommets à la fin de l'été et au début de l'automne. Les indices d'assimilation atteignent un maximum dans le bassin de l'ouest (jusqu'à 3.5 mgC/mg chlorophylle *a* par heure) et un minimum dans le milieu du bassin central et dans le bassin de l'est approximativement 1.4 mgC/mg chlorophylle *a* par heure. Il y a nettement augmentation de l'indice d'assimilation vers l'ouest.

Jusqu'au début de l'été, les deux lacs ont une production primaire à peu près semblable en surface, mais la photosynthèse totale, mgC/m^2 par heure, est plus élevée dans le lac Ontario que dans le lac Erié. En été, le lac Erié a une production plus élevée, tant sur la base de mgC/m^3 par heure que sur celle de mgC/m^2 par heure. Au cours de la période

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avril–décembre, le rendement total du lac Ontario est estimé à 170 gC/m², alors que dans le lac Erié on a trouvé des valeurs de 160, 210 et 310 gC/m² dans les bassins est, central et ouest, respectivement.

Received October 30, 1972 Accepted July 24, 1973

DESPITE recent concern with eutrophication problems in the Great Lakes, studies of primary production are extremely limited in the literature. Lake Erie has been the location of several primary production studies (Verduin 1962; Saunders 1964; Olive et al. 1969; Parkos et al. 1969) but these were limited either to the Western Basin, or to single cruises. Primary production measurements in Lake Ontario are apparently nonexistent except for an indirect value computed by the chlorophyll–light method (Saunders 1964). Thus no comprehensive measurements of primary production have been made on either of these two lakes.

The purpose of this investigation was to perform a comprehensive study of temporal and spatial variations in primary production in lakes Erie and Ontario. Both surface and integral measurements using the ^{14}C method were made on the lakes to compare their productivity in terms of their trophic status.

Methods

Primary production estimates were obtained on 12 cruises between February and December, 1970, from 32 stations (Fig. 1) on Lake Ontario and 25 stations on Lake Erie on 10 cruises between April and December, 1970. A composite water sample consisting of water mixed in equal parts from 1 and 5 m was collected at each station and 100 μl Na_2 $^{14}CO_3$ added in an amount equivalent to approximately 4 μc/l. After mixing for several minutes, the sample was subdivided into 100-ml aliquots and transferred to 125-ml glass-stoppered bottles for incubation. One dark bottle and two light bottles were used at each station, with the exception of the winter and spring cruises on Lake Ontario when only one light bottle was utilized. Samples collected between 1600 and 0600 were held in a deckboard tank kept at lake temperature and primary production measured the following morning to prevent possible harmful effects of sudden exposure of darkened cells to light. The apparatus for incubation consisted of a tank through which surface lake water was continuously pumped. A bank of lights consisting of high-output daylight fluorescent lamps and 40-W incandescent lamps was suspended above the tank. Light intensity from the vertical was approximately 8 klux. After 5-h incubation, the contents of the bottles were filtered through 0.45-μ pore-sized membrane filters and prepared for activity determination using a liquid scintillation counter. Before August, the method of Schindler (1966) was used; subsequently we used Lind and Campbell's (1969) technique. The results of these determinations were used to compute estimates of near-surface primary production rates at each station in mg C/m³ per hour.

In addition to this, on each cruise one in situ experiment of approximately 5-h duration was conducted. Bottles containing 100 ml of water collected at various depths to 15 m were inoculated with ^{14}C and resuspended at the depth collected.

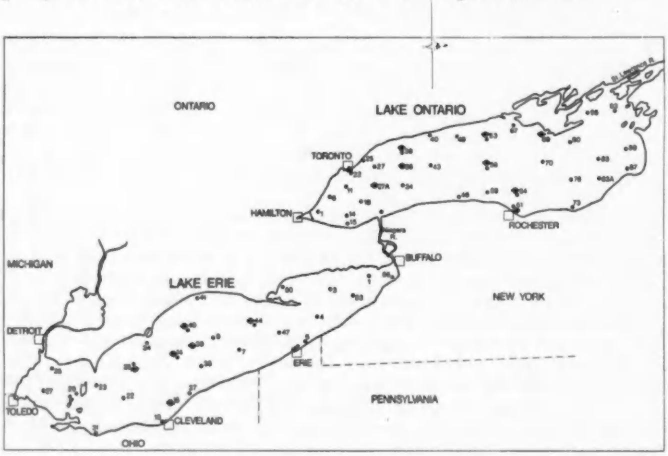

FIG. 1. Map of primary production stations on Lakes Erie and Ontario. ●, indicates incubator production measurements, -●-, in situ measurement.

The results of these experiments were used to compute integral rates of primary production in mgC/m^2 per hour. The ratio of the values obtained aboard ship to these in situ integral values was plotted against Secchi disc depth at the times and stations in question and the relationship was found to be linear with a correlation coefficient equal to $+0.801$ (Fig. 2). The best straight line passing through the origin was then used to extrapolate corresponding average estimates of integral primary production from average Secchi disc and near-surface production values for each cruise and region of the lake within a cruise.

To convert this to daily rates, average hourly rates per square meter by basin for each cruise were multiplied by six to obtain integral production corresponding to a 6-h period. Average day rates were then obtained by multiplying these values by seasonal factors based on approximations of data given in Vollenweider (1965). Factors employed were 1.0 for winter cruises, 1.5 for spring and fall cruises, and 2.0 for summer cruises. The resulting values were then plotted against time and the area of the figure obtained by connecting consecutive points with straight lines was computed to yield an estimate of production per unit surface area for the period of time in question. A lake mean for Lake Erie was obtained by weighting according to basin surface area, using weighting factors of 0.25, 0.63, and 0.12 for Eastern, Central, and Western basins, respectively.

Results and Discussion

PRIMARY PRODUCTION IN LAKE ONTARIO

The surface primary production (1 and 5 m mixed water) of Lake Ontario for each cruise is shown in Fig. 3. To the end of May, highest surface values (mgC/m^3 per hour) occurred in inshore waters, especially along the western shore of the lake from Toronto towards the mouth of the Niagara River. Such production patterns correlated well with the occurrence of the thermal bar in May, inshore of which production was highest (Gächter et al. 1974). Starting in June, a more complex pattern of primary production was observed, but highest values generally occurred in the extreme western end of the lake, and in the eastern regions. For example, between June 22 and 28, the low values along the northern shore were related to upwellings of cold water (Gächter et al. 1974). In November and December, the regions of highest production were similar to those found in the spring along the southern shore.

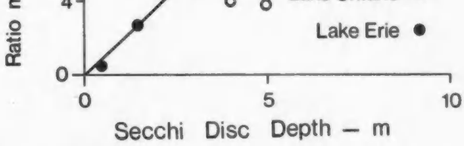

FIG. 2. Relationship between in situ production (mg C/m^2 per hour) and incubator-measured production (mg C/m^3 per hour) and Secchi disk readings in lakes Erie and Ontario.

Surface primary production was consistently greater in inshore waters than offshore at all times except midsummer to early fall when it is consistently lower; essentially the same pattern is observed with integral values (Fig. 4) except that all differences during the spring are relatively much smaller, the summer period during which offshore values are greater than or equal to inshore values begins a month earlier, and the offshore value is slightly higher in December.

The yearly means of surface production for the stations measured are presented in Fig. 5. Highest annual production occurred in the southern portion of the lake east of Rochester, N.Y. to the head of the St. Lawrence River, and in the western end of the lake between Toronto and the Niagara Peninsula area. The lowest production was found in midlake regions which were approximately half as productive on a yearly mean basis. These production gradients were not as pronounced in Lake Ontario as in Lake Erie, which will be discussed later.

PRIMARY PRODUCTION IN LAKE ERIE

The monthly distribution maps of primary production in Lake Erie (Fig. 6) show several trends. In the spring, highest values of production occurred along the southern shore of the lake, generally to the east of Cleveland and in the Western Basin. In the summer and autumn, high production was observed in the Western Basin with another highly productive area near Erie, Pennsylvania. During the December cruise high values were noted along the north and south shores in the Central Basin. Minimum values in the Western Basin were found at the mouth of the Detroit River, probably related to discharge of cold Lake Huron water in the river. Production minima also occurred in the mid-Central and Eastern basins.

The differences in production between the three basins in Lake Erie are quite apparent if their means

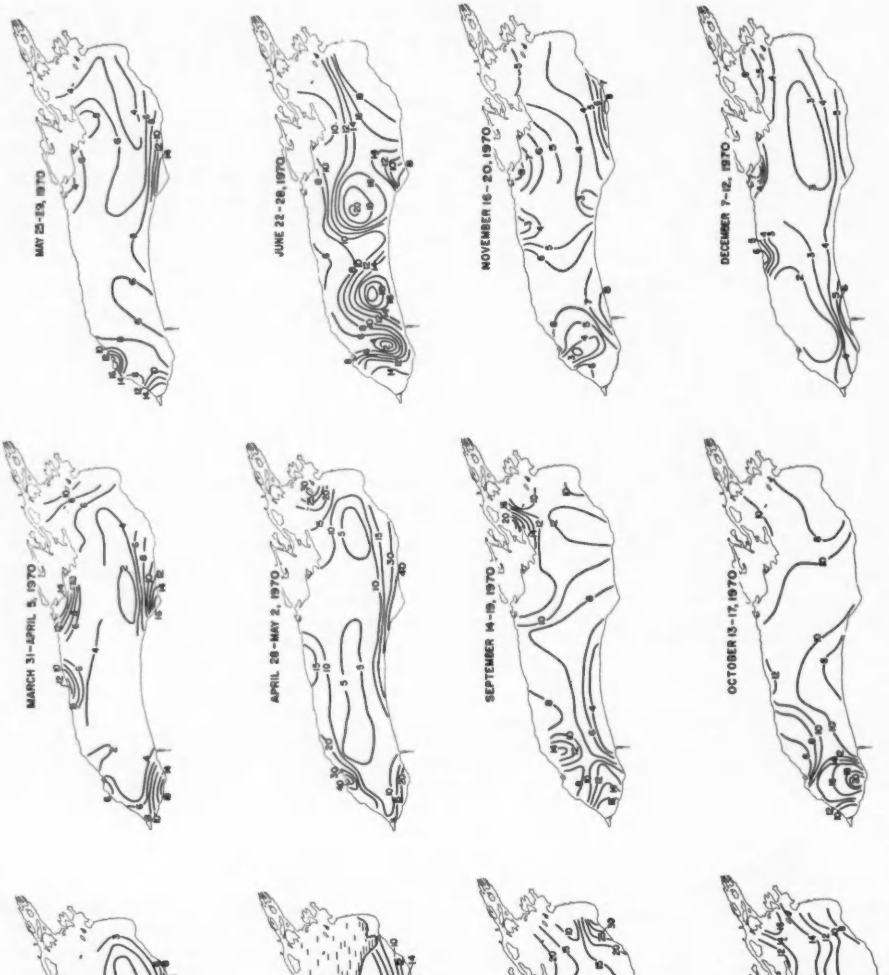
FEBRUARY 3-8, 1970
MARCH 31-APRIL 5, 1970
MAY 25-29, 1970
MARCH 3-9, 1970
APRIL 28-MAY 2, 1970
JUNE 22-26, 1970
JULY 16-20, 1970
SEPTEMBER 14-19, 1970
NOVEMBER 16-20, 1970
AUGUST 17-21, 1970
OCTOBER 13-17, 1970
DECEMBER 7-12, 1970

FIG. 3. Monthly maps of surface primary production, mg C/m³ per hour, in Lake Ontario.

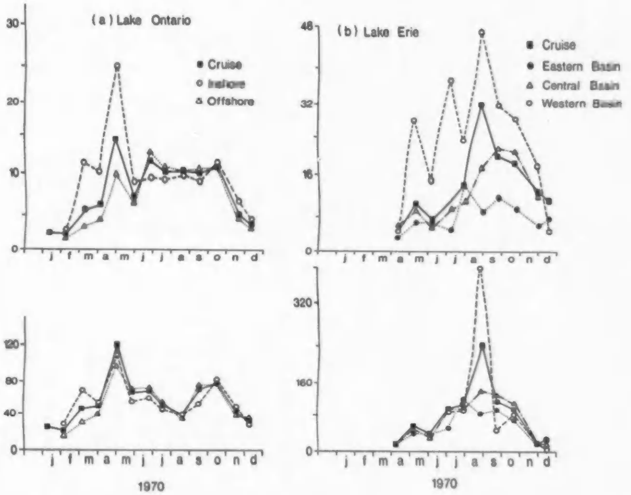

FIG. 4. Monthly primary production values for a) Lake Ontario, inshore and offshore stations, and b) Lake Erie by basin. Ordinate is mgC/m^3 per hour for top graphs and mg C/m^2 per hour for bottom graphs.

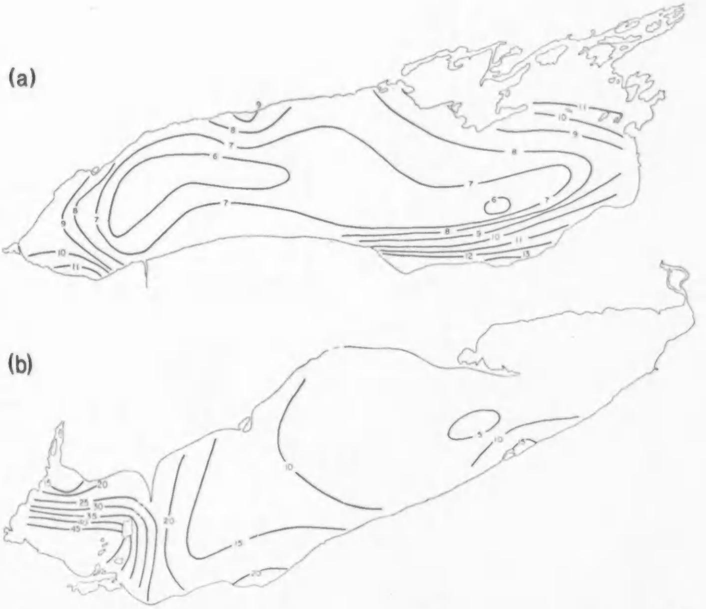

FIG. 5. Mean spatial distribution yearly of primary production, mgC/m^3 per hour for a) Lake Ontario and b) Erie.

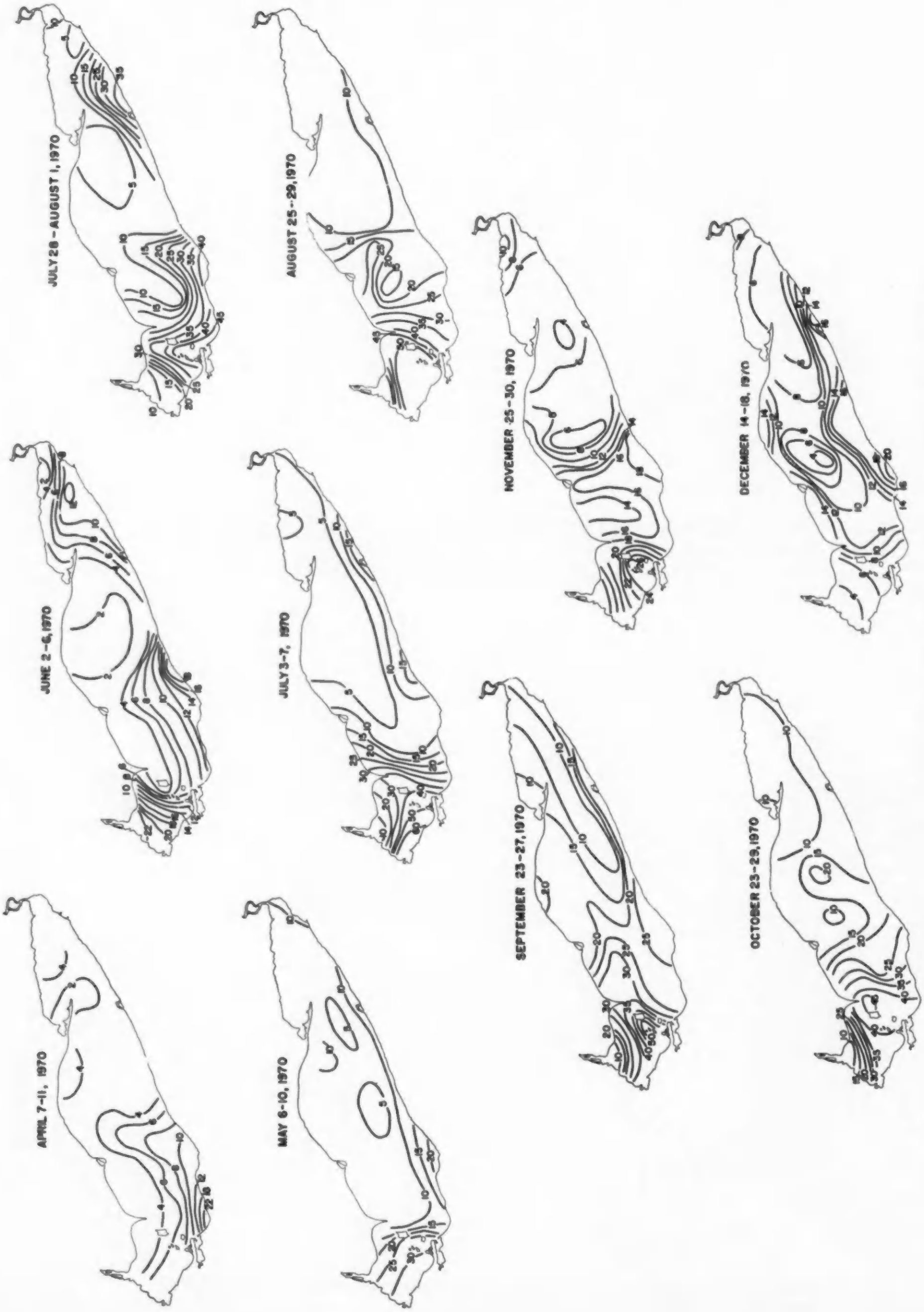
APRIL 7-11, 1970
MAY 6-10, 1970
JUNE 2-6, 1970
JULY 3-7, 1970
JULY 28 - AUGUST 1, 1970
AUGUST 25-29, 1970
SEPTEMBER 23-27, 1970
OCTOBER 23-29, 1970
NOVEMBER 25-30, 1970
DECEMBER 14-18, 1970

FIG. 6. Monthly maps of surface primary production, mg C/m^3 per hour, in Lake Erie.

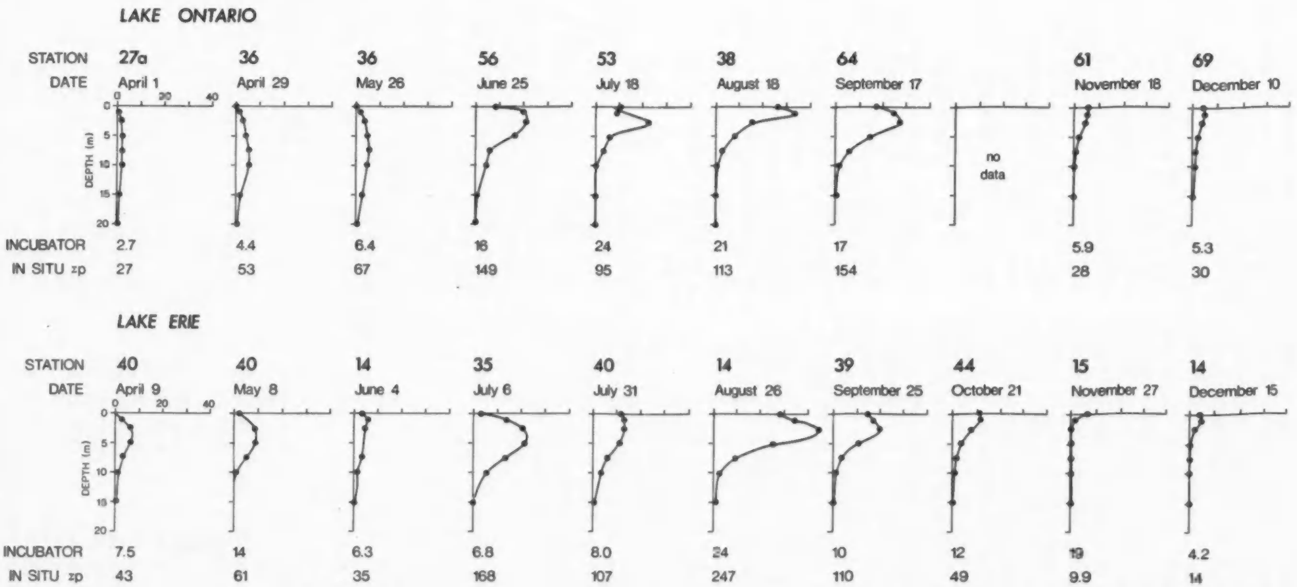

FIG. 7. Monthly profiles of in situ primary production for lakes Erie and Ontario. Stations refer to Fig. 1. Units on abscissa are mgC/m^3 per hour.

are examined on a monthly basis (Fig. 4). With the exception of the April 7–11th and December 14–18th cruises, the Western Basin had the highest primary production (volume basis) with the Eastern Basin least in production. The April and December production was greater in the Central Basin. In terms of integral production, no definite pattern between basins was observed, but the Western Basin was higher in integral production over the year.

The trends in surface production in each of the basins were essentially the same except that the Eastern Basin showed a midsummer decline, giving rise to two small peaks in the early and late summer. Production in the Western Basin reached a maximum in midsummer, and peak production occurred in late summer to early fall in the Central Basin.

In terms of annual average production in Lake Erie (Fig. 5) several generalizations can be made. Highest production occurs in the Western Basin, approximately 40 mgC/m^3 per hour, decreasing easterly to about 5 mgC/m^3 per hour at the boundary of the Eastern and Central basins. The water off Erie, Pa. was a region of high production in contrast to the rest of the eastern half of the lake.

DEPTH PROFILES OF IN SITU PRODUCTION

In situ measurements of primary production were conducted during all cruises (Fig. 1) except Lake Ontario in October when a mooring was lost. Profiles obtained are presented in Fig. 7 along with shipboard incubator results conducted over the same time interval. The depth of maximum photosynthesis usually occurred between 3 and 5 m probably due to photoinhibition above that depth and light limitation below.

TABLE 1. Ratio of Lake Erie to Lake Ontario primary production for corresponding months.

Cruise date	Ratio Lake Erie/Ontario primary production mgC/m^3 per hour	mgC/m^2 per hour
early Apr.	0.80	0.33
early May	0.73	0.47
early June	0.93	0.54
late June	1.00	1.37
mid-July	1.43	2.16
mid-Aug.	3.17	6.21
mid-Sept.	1.94	1.63
mid-Oct.	1.67	1.23
mid-Nov.	2.08	0.42
early Dec.	2.88	0.63

TABLE 2. Estimated daily values of primary production in lakes Ontario and Erie, gC/m^2 per day. Apr.–Dec. row is total estimated production in gC/m^2.

Lake Ontario		Lake Erie				
Date	gC/m^2/day	Date	Weighted mean	Eastern Basin	Central Basin	Western Basin
Apr.–Dec.	170	Apr.–Dec.	210	160	210	310
Jan. 6–12	0.15	Apr. 7–11		0.14	0.15	
Feb. 3–9	0.12	May 6–10	0.47	0.37	0.42	0.92
Mar. 3–8	0.42	June 2–6	0.37	0.31	0.27	0.98
Mar. 31–Apr. 4	0.46	July 3–7	0.99	0.58	1.13	1.06
Apr. 28–May 2	1.08	July 28–Aug. 1	1.22	1.44	1.16	1.09
May 25–29	0.60	Aug. 25–29	1.90	1.01	1.69	4.76
May 22–June 27	0.74	Sept. 23–27	1.00	0.85	1.18	0.40
July 16–20	0.61	Oct. 21–25	0.84	0.19	0.96	0.74
Aug. 17–Sept. 21	0.47	Nov. 25–30	0.15	0.14	0.15	0.14
Sept. 14–19	0.64	Dec. 14–18	0.11	0.14	0.12	0.03
Oct. 13–17	0.71					
Nov. 16–20	0.39					
Dec. 7–11	0.19					

COMPARISON OF LAKE ONTARIO AND ERIE PRODUCTION

The ratio of Lake Erie/Lake Ontario primary production was calculated for both mgC/m^3 per hour and mgC/m^2 per hour on cruises occurring roughly within 2 wk of each other due to ship's schedule (Table 1). Surface production (mgC/m^3 per hour) was the least in Lake Erie up to late June, after which Lake Erie was 1.43–3.17 times more productive based upon averages of all stations measured. Integral photosynthesis followed the same trend, but ratios between the lakes were more extreme. However, in mid-November and December, Lake Erie had approximately half the integral photosynthesis rate of Lake Ontario.

Data on daily and yearly production in the two lakes is given in Table 2. Comparison with comparable data contained in Vollenweider (1968) and Ahlgren (1970) reveals a fair degree of consistency with values for European north temperate mesotrophic or mesoeutrophic lakes. The notable exception is western Lake Erie where the maximum daily yield figure indicates extreme eutrophy.

RELATIONSHIP OF PRIMARY PRODUCTION TO CHLOROPHYLL

The patterns of primary production in lakes Ontario and Erie were related to the distribution of chlorophyll *a*. In Lake Ontario (Fig. 8) correlation coefficients of 0.912 and 0.727 were found when mgC/m^3 per hour were plotted against chlorophyll *a*, uncorrected and corrected for pheopigments, respectively. From such data, assimilation numbers, mgC/mg chlorophyll *a* per hour, the slope of the regression line averaged 1.36 and 1.51, respectively, for uncorrected and corrected chlorophyll *a* values. In Lake Erie (Fig. 8) corrected chlorophyll *a* values gave a greater mean assimilation number, 3.04 mgC/mg chlorophyll *a* per hour compared to 1.93 mgC/mg chlorophyll *a* per hour for uncorrected data. The reason for the lower correlation coefficients in Lake Erie is unknown, but may be due to differences in species composition of algae in the two lakes. In our discussion, assimilation numbers uncorrected for pheopigments will be used for the sake of consistency as other authors have not corrected their pigment data.

Comparing the seasonal changes in assimilation number in the two lakes (Fig. 9), highest numbers occurred in the late summer and early fall in Lake Ontario, whereas Lake Erie showed a bimodal distribution with a peak in early May and one in midsummer. The differences between the two lakes may be explained by interaction between different temperature and nutrient conditions in the two lakes (Gächter et al. 1974).

No definite trends of the distribution of annual average assimilation number (chlorophyll *a* uncorrected) were seen in Lake Ontario (Fig. 10). Such ratios were fairly uniform between approximately 1.2 and 1.6. However, in Lake Erie (Fig. 10), highest assimilation ratios were found in the Western Basin and in the southern shore of the Central Basin, centered at Cleveland. Along a west to east transect of the lake, ratios decreased to the middle of the Central Basin and increased again slightly towards the Eastern Basin.

The use of assimilation ratios to interpret patterns of primary production in lakes Erie and Ontario may have some value, especially in relation to nutrient status. Examples of the control of assimilation numbers by nutrients are supported

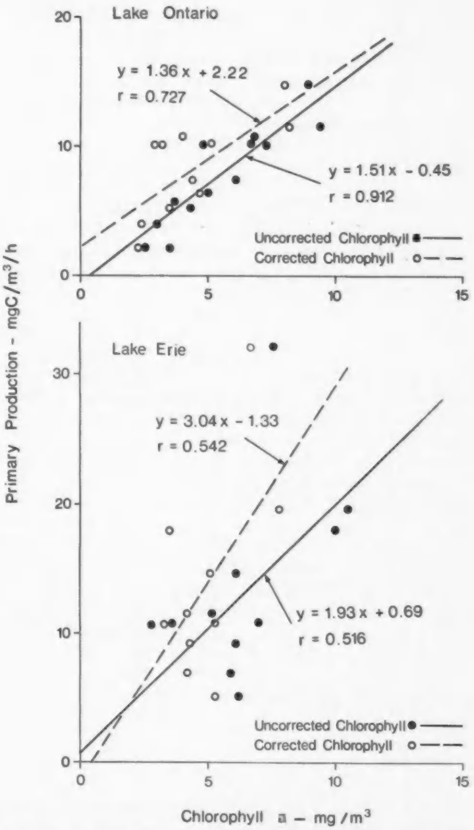

FIG. 8. Primary production-chlorophyll relationships in lakes Ontario and Erie.

in the literature. For example, Holmes (1958) found highest assimilation numbers in the Eastern Pacific Ocean (>7) in nutrient-rich waters, whereas such numbers averaged 2 in other waters. Antia et al. (1963) found high correlations between nutrients and assimilation numbers in enrichment experiments conducted in large-volume plastic spheres. Anderson (1964) found highest numbers in Northern Pacific waters when upwelling was present. Curl and Small (1965) and Thomas (1969, 1970) found similar results in the Pacific Ocean. Increased assimilation numbers upon nutrient enrichment of water samples collected in Oregon coastal waters was demonstrated by Glooschenko and Curl (1971), especially when nutrient levels were lower in water.

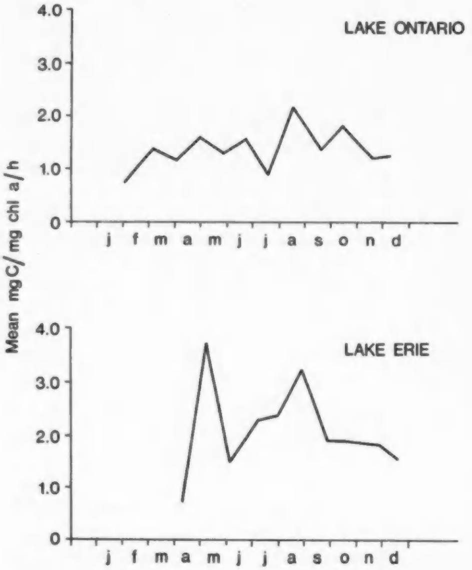

FIG. 9. Mean monthly assimilation numbers, mg C/mg chlorophyll *a* per hour for Lake Ontario and Lake Erie.

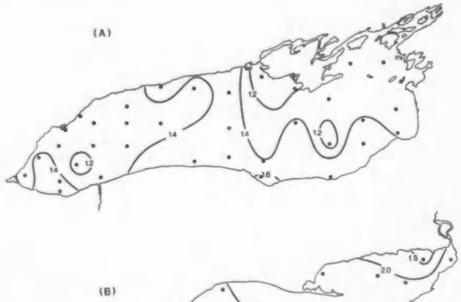

FIG. 10. Mean April–December assimilation number, mgC/mg chlorophyll *a* per hour (uncorrected chlorophyll *a*) in lakes Ontario and Erie. Dots indicate stations sampled.

Our work showed Lake Erie assimilation numbers to be higher than those in Lake Ontario except in the month of April (Fig. 9), which may be an indication of the higher nutrient status of Lake Erie. The highest average assimilation numbers in Lake Ontario are less than the lowest numbers found in Lake Erie. Within Lake Erie, the gradient of such ratios also appears to correlate well with nutrient distributions (Gächter et al. 1974). Temperature does not appear to affect such assimilation numbers as such patterns do not coincide with known temperature gradients in the lake during a given cruise.

Species composition may be important in affecting assimilation numbers. Findenegg (1966) found nannoplankton to assimilate more carbon per unit of biomass than large diatoms or blue-green algae, and also found increasing population density to diminish relative assimilation rates. We did not observe the latter effect in our data, nor did Ahlgren (1970). For example in Lake Ontario, the highest assimilation numbers occur during the late summer. During this period, a high percentage of Chlorophyta and Cyanophyta are present (Munawar and Nauwerck 1971). The lowest assimilation numbers occur during those times of the year when diatoms are abundant. However, on a lakewide basis, the highest assimilation numbers occur when water temperatures are highest. Thus it is hard to separate the interaction in the field between temperature, species composition, and assimilation number. In Lake Erie, species composition data also show highest assimilation numbers when Cyanophyta were abundant in the late summer, whereas in the spring when assimilation ratios were lowest, diatoms were most abundant. Similar patterns were found in Lake Norrviken, Sweden, by Ahlgren (1970) who found highest assimilation numbers when Cyanophyta were dominant in August.

The assimilation numbers that we calculated for the two lakes were lower than those found in the oceanographic literature previously mentioned. Curl and Small (1965) felt that ratios less than 3 indicated nutrient depletion; 3–5, borderline deficiency; and between 5 and 10, nutrient-rich conditions, based upon their work and that of others. By those standards even the highly eutrophic Western Basin of Lake Erie would not indicate nutrient abundance. This discrepancy may be due to inherent differences between marine and freshwater phytoplankton communities, or our incubator technique used for determining such assimilation ratios. We feel, however, that the observed patterns of high assimilation number correlate well with higher nutrient distribution (Gächter et al. 1974) and that mean assimilation ratios above 2 indicate nutrient enrichment in our studies.

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Spatial and Temporal Distribution of Chlorophyll *a* and Pheopigments in Surface Waters of Lake Erie

WALTER A. GLOOSCHENKO, JAMES E. MOORE, AND RICHARD A. VOLLENWEIDER

Department of the Environment, Fisheries and Marine Service
Great Lakes Biolimnology Laboratory
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

GLOOSCHENKO, W. A., J. E. MOORE, AND R. A. VOLLENWEIDER. 1974. Spatial and temporal distribution of chlorophyll *a* and pheopigments in surface waters of Lake Erie. J. Fish. Res. Board Can. 31: 265–274.

Chlorophyll *a* analyses including pheopigments were made on water samples taken on 10 cruises on Lake Erie between April and December, 1970. The highest mean chlorophyll *a* values of approximately 11 μg/liter occurred in the mid-Western Basin, with a second maximum of 6 μg/liter off Erie, Pennsylvania. The southern shore is also characterized by high values of chlorophyll to the east of Cleveland, Ohio. The lowest yearly means were found in the eastern portion of the Central Basin and most of the Eastern Basin (approximately 3 μg/liter.) Ratios of chlorophyll *a* between the Eastern, Central, and Western basins have a yearly mean of 1:1.4:2.8, respectively; with maximum differences in the summer, i.e. late August, the ratio was 1:1.5:7.2.

Pheopigment concentration in the surface waters reached a maximum in late October corresponding to the fall overturn of the lake and subsequent resuspension of organic matter containing degradation products from the bottom of the lake. No significant correlation was found between zooplankton abundance and pheopigment concentration as in other water bodies studied. This may indicate that zooplankton food chains are primarily detrital in Lake Erie, with grazing of living phytoplankton playing a lesser role compared with more oligotrophic water bodies.

GLOOSCHENKO, W. A., J. E. MOORE, AND R. A. VOLLENWEIDER. 1974. Spatial and temporal distribution of chlorophyll *a* and pheopigments in surface waters of Lake Erie. J. Fish. Res. Board Can. 31: 265–274.

Des analyses de chlorophylle *a*, incluant les phéopigments, ont été effectuées sur des échantillons d'eau prélevés au cours de 10 croisières dans le lac Erié d'avril à décembre 1970. Des valeurs moyennes maximales de chlorophylle *a* d'environ 11 μg/litre ont été observées dans le centre du bassin ouest, avec un deuxième maximum de 6 μg/litre au large d'Erié, Pennsylvania. La rive sud est également caractérisée par de hautes teneurs en chlorophylle à l'est de Cleveland, Ohio. Les plus basses moyennes annuelles se trouvent à la partie est du bassin central (environ 3 μg/litre). Les rapports de la chlorophylle *a* entre les bassins de l'est, du centre et de l'ouest ont une moyenne annuelle de 1:1.4:2.8 respectivement; avec différences maximales en été, i.e. à la fin d'août, alors que le rapport est de 1:1.5:7.2.

La teneur en phéopigments des eaux superficielles atteint un maximum à la fin d'octobre, correspondant au brassage général d'automne et resuspension subséquente de la matière organique contenant des produits de dégradation du fond du lac. Nous n'avons pas trouvé de corrélation significative entre l'abondance du zooplancton et la teneur en phéopigments, comme ce fut le cas dans d'autres masses d'eau étudiées. Ceci peut être une indication que les chaînes alimentaires zooplanctoniques sont avant tout détritiques dans le lac Erié, le broutage du phytoplancton vivant jouant un rôle de moindre importance, comparativement aux masses d'eau plus oligotrophes.

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PHYTOPLANKTON research on Lake Erie (Davis 1966, 1969a; Sweeney 1970) has been concerned mainly with taxonomic studies emphasizing seasonal cycles and species uccessions in the Western Basin of the lake (Chandler 1940, 1944; Chandler and Weeks 1945; Verduin 1960). Other studies have been limited to nearshore waters such as Davis (1964) and Michalski (1968). Lakewide

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studies, especially in the Eastern Basin, have been limited. Hartley and Potos (1970) have presented data on distribution of major groups of algae during four cruises on 20 midlake stations from May 1967 to January 1968, and on 17 Ohio domestic water intakes. Munawar et al. (1973) have intensively studied the distribution of phytoplankton from April through December, 1970, over the entire lake.

No comprehensive studies have been made on the temporal and spatial distribution of chlorophyll *a* and its pheopigments in Lake Erie. The present study examines this distribution with special reference to the pheopigment cycle in the lake.

Materials and Methods

The sampling program was carried out between April and December, 1970, for a total of 10 cruises. Water samples were collected on 8 stations in the Eastern Basin, 12 in the Central Basin, and 5 in the Western Basin during each cruise, with Van Dorn bottles at depths of 1 and 5 m. Samples from these two depths were mixed together in equal parts, and filtered through a Whatman GF/A glass fiber filter to which five drops of an $MgCO_3$ suspension was added. Filters were then kept until analysis at –10 C.

Filters were ground with a teflon homogenizer for 1 min in 3 ml 90% acetone, made to 10.0 ml volume, and placed in the dark at room temperature for 1 h to improve extraction. After centrifugation for 10 min at 3000 rpm, chlorophyll *a* was spectrophotometrically determined by the method and equations of Strickland and Parsons (1968), and pheopigments by the method of Lorenzen (1967a).

Vertical tows of zooplankton were made at each station with spectacle nets (73 μ mesh, 0.126 m^2 area) from a depth of 2 m off the bottom to the surface. The samples were counted by Coulter Counter (Sheldon and Parsons 1967).

Results

AREAL DISTRIBUTION OF CHLOROPHYLL *a* IN LAKE ERIE

The average chlorophyll *a* values for the April–December period on the lake are summarized in Fig. 1. Several evident features can be noted. The maximum average values of approximately 11 μg/liter lie in the mid-Western Basin. From that point, chlorophyll *a* gradients decrease towards the Detroit River mouth and towards the Central Basin. Another maximum of 6 μg/liter is located at Erie, Pa. In the Central Basin, highest values lie along the Western Basin boundary in a north–south direction. However, chlorophyll *a* contours then shifted more parallel to the shoreline indicating the possibility of combined effects of temperature and nutrient discharge. The Eastern Basin is very low in chlorophyll *a* with slightly higher values along the southern shore and in the eastern end of it towards Buffalo, N.Y.

Lakewide distribution of chlorophyll *a* between April and December, 1970 (corrected for pheopigments) is presented in Fig. 2. During April 7–11, values were relatively low over most of the lake, with lowest values in the Eastern Basin and at the mouth of the Detroit River; both of these minima are probably influenced by low water temperatures caused by the presence of ice. The highest values were found in the mid-Western Basin and regions of inshore warming, especially in areas subjected to high nutrients such as the region east of Sandusky Bay and the vicinity of Erie, Pa.

In early May chlorophyll *a* values were generally much lower than the previous month. This may be due to the decline of the spring pulse in the Western Basin and adjacent Central Basin. The maximum in the eastern half of the Central Basin can be explained as the spring pulse of phytoplankton, as such a pulse appears to start in the Western Basin before April and progresses eastward towards the Eastern Basin where the pulse occurred in 1970 between the early May and June cruises. This phenomenon will be discussed in more detail later in the paper.

By early June, the spring pulse was noted in the Eastern Basin with correspondingly higher chlorophyll concentrations. Gradients of this pigment decreased easterly from the Western Basin where a minima occurred in the mid-Central Basin. The latter represents the beginning of the summer minima in the Central Basin. In early June the summer minima was evident in the entire Central and Eastern basins, but extremely high values of chlorophyll *a* were noted in the Western Basin. Three weeks later in late July–early August, the chlorophyll maxima in the Western Basin shifted towards the eastern part of that basin. Two other evident maxima were noted at Cleveland, Ohio, and Erie, Pa. These may have been related to nutrient discharge from these two cities.

In late August maximum values of chlorophyll *a* in Lake Erie for the year were found. These were in the Western Basin, especially in the central part. Slight increases of chlorophyll *a* in the other basins were evidence of the beginning of the fall phytoplankton pulse. By late September, the fall pulse was at its maximum, and chlorophyll *a* values decreased again in an easterly direction. By late October the Eastern Basin was quite low in chlorophyll *a* and this trend continued into December. During late autumn and into mid-December, highest values of chlorophyll *a* occurred from

Sandusky Bay to the east of Cleveland, again probably related to municipal waste discharges.

COMPARISON OF CHLOROPHYLL *a* IN LAKE ERIE BASINS

Average chlorophyll *a* values for each basin are given in Fig. 3. The highest values of chlorophyll *a* occur in the Western Basin reaching a peak during late summer. The absence of a spring maximum in the Western Basin is most likely due to the first sampling cruise being in April, and the pulse occurring earlier. The Central Basin shows indication of the end of a pulse in early April, a summer minimum existing through July, with a fall pulse peaking in late September. The Eastern Basin has no definite pigment cycle, but individual station data indicates a bimodal trend.

Ratios of mean chlorophyll *a* values in the three basins are given in Table 1. The basins were similar in chlorophyll *a* content in April. The lower values in the Central Basin compared to the Eastern Basin in May and June are indicative of the summer minimum in the Central Basin. A greater difference is found between the Western Basin and the Central Basin (2:1) than between the Central and Eastern basins (1.4:1). The lack of samples before April 1970 could change ratios over the year if significantly higher chlorophyll *a* occurred in the spring pulse in the Western Basin than in the Central Basin.

SEASONAL CYCLES OF CHLOROPHYLL *a* AND PHEOPIGMENTS IN RELATION TO ZOOPLANKTON

Data were analyzed from all stations in the three basins to investigate the relationship between total

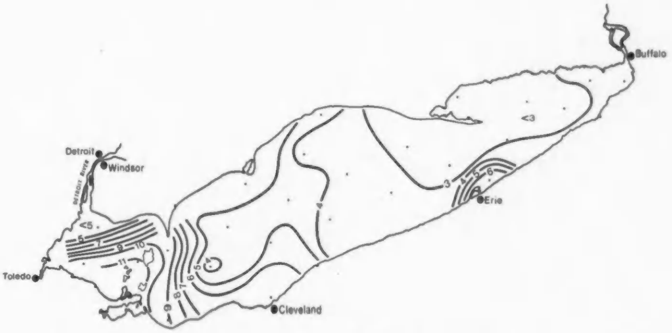


FIG. 1. Average chlorophyll *a* (μg/liter), April–December, 1970.

TABLE 1. Average chlorophyll *a* (μg/liter) in Lake Erie basins by month with ratios calculated between basins — 1970.

Cruise	Basin			Ratio of E:C:W Basin
	Eastern	Central	Western	
Apr. 7–11	4.1	5.3	5.9	1:1.3:1.4
May 6–10	3.5	2.9	4.4	1:0.8:1.3
June 2–6	5.4	2.7	5.9	1:0.5:1.1
July 3–7	1.5	2.5	11.9	1:1.7:7.9
July 28–Aug. 1	4.4	3.7	9.8	1:0.8:2.2
Aug. 25–29	2.7	4.1	19.3	1:1.5:7.2
Sept. 23–27	4.7	9.2	10.2	1:1.9:2.2
Oct. 21–25	1.4	3.0	7.8	1:2.1:5.6
Nov. 25–30	2.7	5.4	7.6	1:2.0:2.8
Dec. 14–18	2.6	5.7	3.3	1:2.2:1.3
Apr. 1–Dec. means	3.2	4.4	8.9	1:1.4:2.8
No. stations	8	12	5	

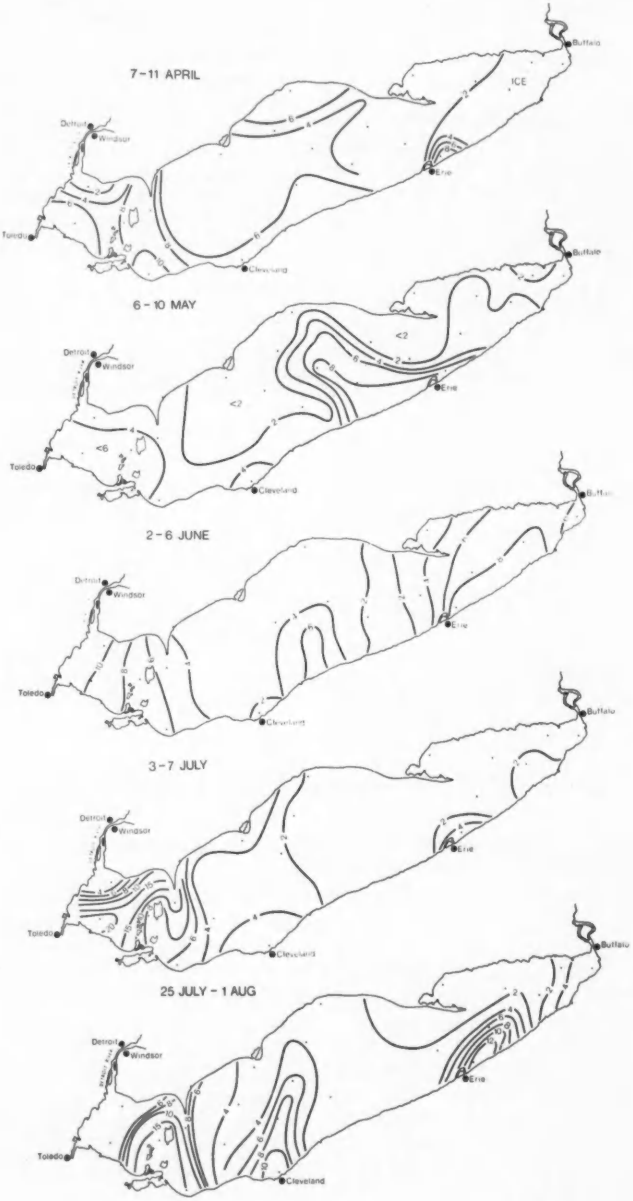
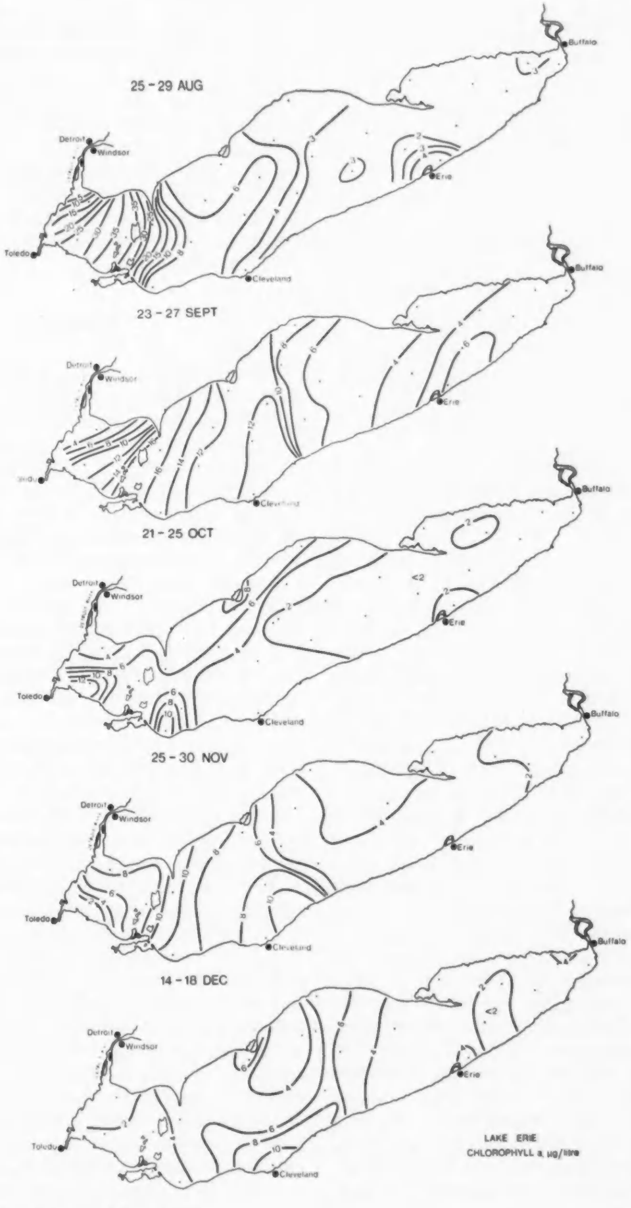

7-11 APRIL
ICE
6-10 MAY
<2
<6
2-6 JUNE
3-7 JULY
25 JULY - 1 AUG
Detroit
Windsor
Toledo
Cleveland
Erie
Buffalo

FIG. 2. Monthly distribution of


25 - 29 AUG
23 - 27 SEPT
21 - 25 OCT
25 - 30 NOV
14 - 18 DEC
Detroit
Windsor
Toledo
Cleveland
Erie
Buffalo
LAKE ERIE
CHLOROPHYLL a, μg/litre

chlorophyll *a*, (μg/liter) in Lake Erie, 1970.

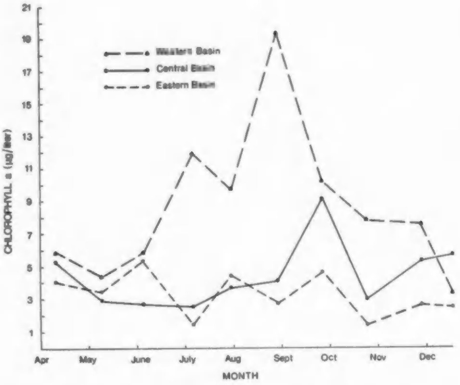


FIG. 3. Seasonal distribution of chlorophyll *a* in Lake Erie, 1970, by basin average.

chlorophyll *a* and zooplankton biomass. In this paper, data are discussed for several selected stations which we consider to be representative of their respective basins.

The mid-Eastern Basin as depicted on station 3 shows the classical bimodal pattern of phytoplankton development with peaks in early June, a summer minimum, and late September peak (Fig. 4a). The amount of pheopigment was highest in early July, coinciding with the zooplankton peak, and in late October during overturn (Table 2). In general, this trend was seen on most Eastern Basin stations — a bimodal distribution of chlorophyll *a*, and pheopigment peaks corresponding to the zooplankton maximum and fall overturn.

The Central Basin is somewhat similar to the Eastern Basin. The selected station, station 9 (Fig. 4b), located in the middle of the Basin, again has a bimodal pattern. However, the spring pulse occurs earlier in May. A high percentage of pheopigments was observed during the fall overturn, but little relationship was seen between zooplankton abundance and pheopigment formation in July. Near the southern shore (Fig. 4c) the spring pulse occurred sometime before the April sampling date. Highest pheopigments were present during the zooplankton peak and during the fall overturn. In the Central Basin, data indicated that the spring pulse began before April in inshore waters and midbasin waters in the western part of this basin. The pulse in midlake waters, especially in the eastern end of the Central Basin, occurred later in the season in June.

The Western Basin seasonal cycle is represented by station 27 (Fig. 4d). Unfortunately, zooplankton sampling in Western Basin stations did not coincide with phytoplankton sampling, so such data are unavailable.

The annual cycle of pheopigments and zooplankton in the three basins is summarized in Fig. 5. In the Central Basin, a small pheopigment peak occurs in the late spring–early summer, corresponding with the zooplankton peaks for these basins. The percentage of these pigments compared to total chlorophyll *a* is somewhat higher also as given in Table 2. However, the major amount of pheopigments in the surface waters of the basins occur in late October coinciding with the fall overturn of the lake.

Discussion

Previous studies in Lake Erie by Chandler (1940, 1942, 1944), Chandler and Weeks (1945), and Davis (1954, 1962) have shown phytoplankton maxima in the spring and fall, with winter and summer minima. This bimodal pattern has been reported as being typical of large temperate lakes (Hutchinson 1967). Smaller lakes usually have a more complicated succession of maxima and minima. Davis (1964) studied phytoplankton counts available from a Cleveland water plant intake from 1919–63 and concluded vernal and autumnal phytoplankton maxima have consistently become more intense, and summer and winter minima less well marked and shorter in duration. In some of the later years, winter minima failed to develop. Michalski (1968), studying Canadian inshore waters of Lake Erie, found a classical bimodal phytoplankton development with no extended spring and fall maxima. In the Central Basin, he found no definite minima in the winter or definite spring maxima, whereas in the Eastern Basin he found results similar to those previously mentioned by Davis (1964).

In terms of our research, a definite bimodal pattern of phytoplankton was found in the Central and Eastern basins. The spring maxima occurred before the April 6–11 sampling date in inshore waters of the Central Basin and in the deeper waters in the western portion of that basin. By December, the autumnal maxima had not yet significantly declined, nidicating a prolongation of the autumnal maxima especially in inshore waters. The date of the spring maximum appears to occur later during the season in waters last to warm up. In the Western Basin, seasonal cycles were characterized by a large prolonged single maxima in the late summer–early autumn. The exception to this pattern was located at the station at the mouth of the Detroit River where a classical bimodal pattern was seen.

Comparisons of standing crop of phytoplankton in the three basins are quite limited. Davis (1966)

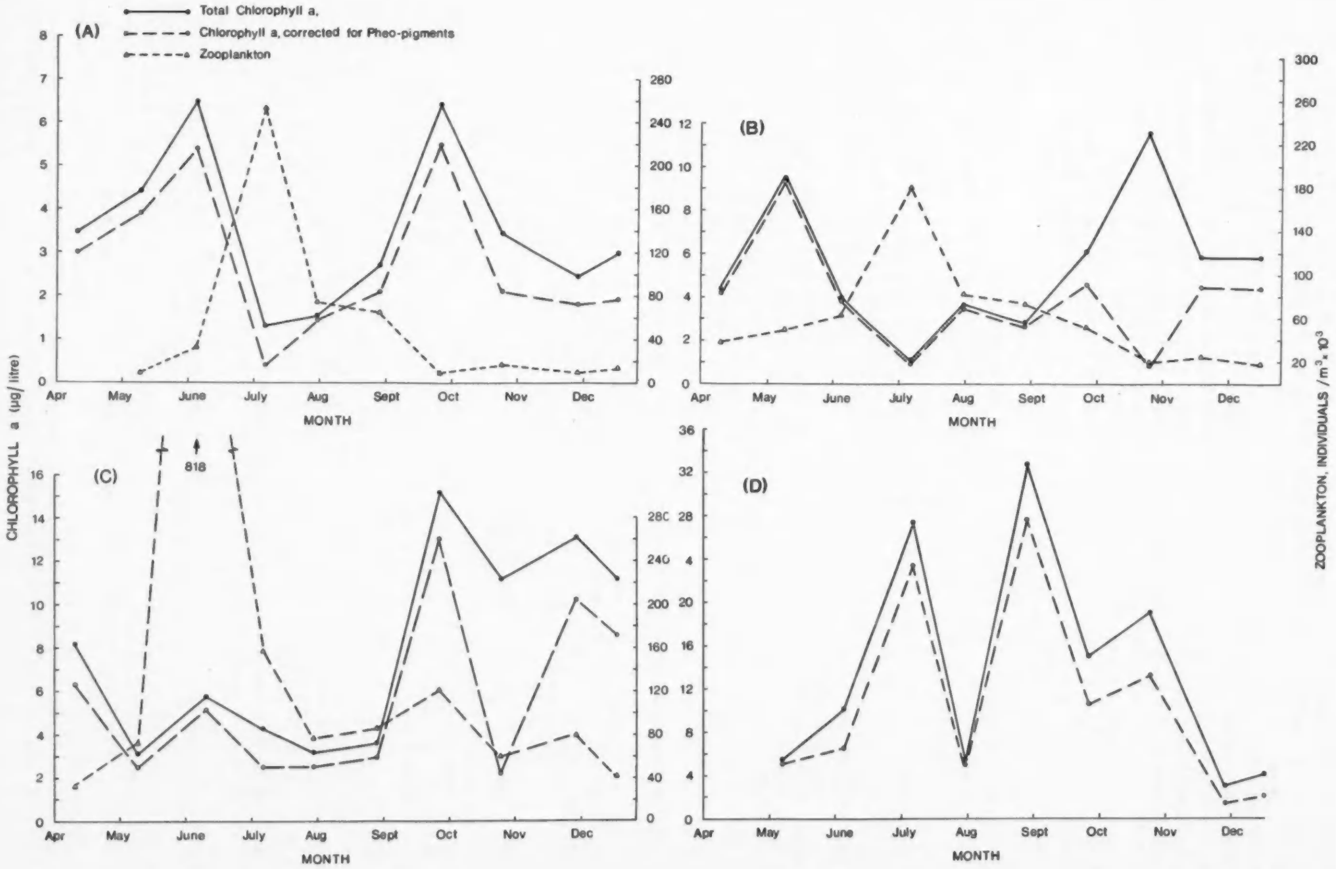


FIG. 4. Seasonal distribution of total chlorophyll *a* (●), chlorophyll *a* (○), and zooplankton (△) in Lake Erie for (a) station 3, mid-Eastern Basin, (b) station 9, mid-Central Basin, (c) station 37, south shore of Central Basin, and (d) station 27, Western Basin, Lake Erie.

gives a ratio of chlorophyll *a* in October 1967 of 1:1.5:4.7, whereas Michalski (1968) gives a summer 1967 ratio of 1:1.5:5.2 E:C:W: based upon asu per ml (areal standard unit = $400\ \mu^2$). Our values are fairly similar to those of Michalski for the summer. However, our work indicated that basin ratios are dependent upon the sampling date. We found in a period of a month such ratios can change drastically; for example, in early June, the E:C:W: ratio was 1:0.5:1.1 whereas in early July, a ratio of 1:1.7:7.9 was noted. Such work indicates that a monthly sampling interval is too long to interpret seasonal cycles in the lake especially during the summer. Also, the lack of sampling between December and April seriously limits understanding of such cycles as this seems to be the time during which the spring maxima occurs in the western half of the lake and in inshore waters.

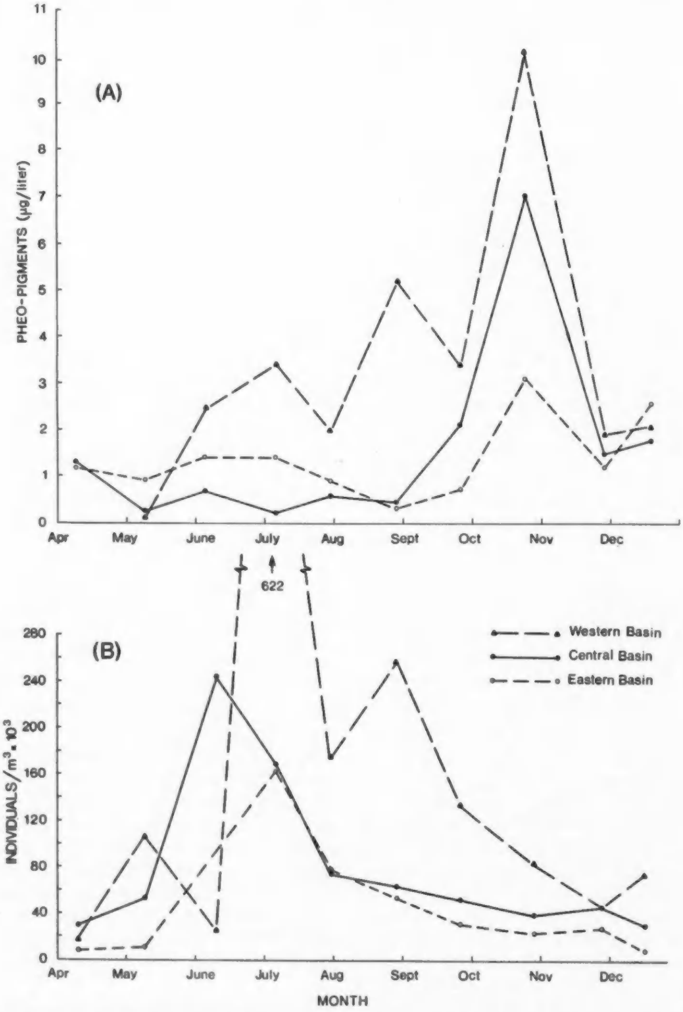


FIG. 5. Seasonal distribution of (*a*) pheopigments, and (*b*) zooplankton in Lake Erie, 1970 by basin average.

The seasonal cycle of pheopigments also is of interest in Lake Erie. Studies on Lake Ontario by Glooschenko et al. (1972) found the highest pheopigment occurrence was at the time of the zooplankton peak in the late summer. A positive correlation of + 0.896 was found in Lake Ontario between pheopigment concentration and zooplankton abundance, which doesn't imply necessarily a causal relationship. However, other studies by Blumer and Thomas (1965), Currie (1962), Lorenzen (1965, 1967b), Moreth and Yentsch (1970), and Yentsch (1965) showed the importance of zooplankton in the degradation of chlorophyll *a* to its associated pheopigments.

In relatively shallow lakes no correlation was found between pheopigments and zooplankton by Moss (1970). He found no correlation between pheopigments and chlorophyll *a* nor an accumulation of such pigments with depth. He suggested that sediment resuspension accounted for occurrence of pheopigment in the seston in shallow ponds.

The pattern of pheopigment distribution observed in Lake Erie (Fig. 5) is similar to that observed by Moss (1970). Even though slightly higher pheopigments occurred in the Central Basin during the zooplankton peak (Fig. 4), the highest concentration of pheopigments occurred in late October coinciding with the fall overturn of the lake. This is possibly due to resuspension of bottom sediments and subsequent release into the water column of degraded organic matter with contained pheopigments. Such resuspension was postulated by Kemp (1971) and also documented during Project HYPO by Blanton and Winklehofer (1971). Since Lake Erie is shallow (mean depth 21 m), such a mechanism appears quite reasonable to explain the fall pheopigment peak observed.

Another possible explanation for the lack of correlation between zooplankton abundance and the presence of pheopigments in surface waters could be the nature of zooplankton feeding habits. Gliwicz (1969) studied feeding habits of zooplankton in six Polish lakes ranging from oligotrophy to eutrophy. He found in eutrophic lakes the larger types of phytoplankton present were unavailable to zooplankton which utilized mainly detritus or bacteria. He also found higher percentages of cladocerans and rotifers and decreased numbers of calanoid copepods. Gannon (1972) studied zooplankton in Lake Michigan, and in eutrophic regions such as Green Bay found increased abundance of cladocerans and rotifers with calanoid copepods predominating offshore water.

Watson and Carpenter (1974) compared the zooplankton of lakes Erie and Ontario and found in the more eutrophic waters of Lake Erie higher numbers of cladocerans (Davis 1966). Davis (1969b) showed that the highly eutrophic portions of Lake Erie were characterized by protozoans, rotifers, and cladocerans rather than copepods. Since the zooplankton of eutrophic Lake Erie might be expected to preferably utilize detritus and bacteria as opposed to grazing upon live phytoplankton, one would not expect to find a high correlation between zooplankton abundance in this lake and pheopigment formation due to grazing. This fact, along with resuspension of degradation products of chlorophyll *a*, would explain the differences in the pheopigment cycles of Lake Erie and that of Lake Ontario previously described by Glooschenko et al. (1972).

Acknowledgments

We wish to thank several persons for their assistance with the research project. These include J. Leslie for his Coulter Counter analyses and field assistance, R. Collins and G. Carpenter for their help with chlorophyll analyses and field sampling, and Dr N. Watson for his comments on zooplankton. In addition, the members of the Technical Operations Section, CCIW, and the crew of the MV *Martin Karlsen* are thanked for their contributions to the sampling program.

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Seasonal Variations of Temperature and Nutrients in the Surface Waters of Lakes Ontario and Erie

R. GÄCHTER,[1] R. A. VOLLENWEIDER, AND W. A. GLOOSCHENKO

Department of the Environment
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

GÄCHTER, R., R. A. VOLLENWEIDER, AND W. A. GLOOSCHENKO. 1974. Seasonal variations of temperature and nutrients in the surface waters of lakes Ontario and Erie. J. Fish. Res. Board Can. 31: 275–290.

During 1970, temperature and nutrient distributions were measured in surface waters of lakes Ontario (12 cruises) and Erie (10 cruises). Nutrient patterns are compared and discussed in relation to temperature, primary production, and nutrient sources.

In Lake Erie, due to the early onset of the phytoplankton spring bloom, nutrient concentration started to decrease much earlier than in Lake Ontario. During spring, patterns of nutrients, chlorophyll *a*, and primary production were influenced by the thermal bar in Lake Ontario. In Lake Erie the nutrient supply controlled such patterns. In Lake Erie inorganic nutrients were depleted lake-wide in summer; in Lake Ontario, nutrients were highest in regions where upwelling occurred or inputs were high. Due to the earlier onset of fall overturn in Lake Erie, the nutrient concentration started to increase earlier in the fall than in Lake Ontario.

GÄCHTER, R., R. A. VOLLENWEIDER, AND W. A. GLOOSCHENKO. 1974. Seasonal variations of temperature and nutrients in the surface waters of lakes Ontario and Erie. J. Fish. Res. Board Can. 31: 275–290.

Au cours de 1970, nous avons étudié la distribution des températures et des substances nutritives dans les eaux de surface des lacs Ontario (12 croisières) et Erié (10 croisières). Nous comparons dans ce travail les caractéristiques de la répartition des substances nutritives en relation avec la température, la production primaire et les sources de substances nutritives.

Dans le lac Erié, par suite de l'arrivée hâtive de la poussée printanière du phytoplancton, la concentration des substances a commencé à diminuer plus tôt que dans le lac Ontario. Au printemps, la distribution des substances nutritives, la chlorophylle *a* et la production primaire ont été influencées par la barrière thermique dans le lac Ontario. Dans le lac Erié, cette distribution a été contrôlée par l'approvisionnement en substances nutritives. Dans le lac Erié, les substances nutritives inorganiques étaient épuisées à la grandeur du lac en été; dans le lac Ontario, les substances nutritives étaient à leur maximum dans les régions de remontée d'eaux profondes ou là où les apports étaient abondants. A cause du début plus hâtif du brassage général d'automne dans le lac Erié, la concentration des substances nutritives a commencé à augmenter plus tôt à cette saison que dans le lac Ontario.

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IN this paper, a summary is given of surface temperature distribution and selected chemical parameters which are directly related to production measurements, i.e. total and soluble reactive phosphorus, inorganic nitrogen (nitrate + ammonia), and reactive silica. It is intended to supplement phytoplankton studies conducted during the same period, the results of which are presented in several papers, i.e. Glooschenko et al. (1974a), primary production; Glooschenko et al. (1972a, 1973, 1974b), chlorophyll *a*; Munawar and Nauwerck (1971), phytoplankton composition; also Vollenweider et al. (1974).

This paper in no sense can or will substitute for more complete studies on the nutrient chemistry of lakes Ontario and Erie, which are underway at the Canada Centre for Inland Waters (CCIW). However, two facts justify this summary: a) the relations which could be shown to exist between certain production patterns and nutrient chemistry and b) no other chemical data exist for Lake Ontario

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[1] Present address: Hydrobiological Laboratory der EAWAG-ETH CH-6047, Kastanienbaum, Switz.

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during 1970, the only year for which we have a complete production study thus far. Accordingly, the paper has to be read with the previously mentioned papers on biology.

Methods

During 1970, monthly monitor cruises were carried out in Lake Ontario (February–December) and Lake Erie (April–December). Samples from 1- and 5-m depths were taken at 32 stations in Lake Ontario and 25 stations in Lake Erie (Fig. 1). The two samples obtained at each station were mixed and used for measuring primary production and chlorophyll (cf. Glooschenko et al. 1972a, b, 1974a, b). Chemical analyses on these samples performed by the Water Quality Laboratory of CCIW on board ship or at the main laboratories included total phosphorus, soluble reactive phosphorus, nitrate, ammonia, and soluble reactive silica. Routine measurements included alkalinity, *p*H, and conductivity. Analytical procedures are summarized by Traversy (1971). Temperature profiles have been obtained by bathythermography technique. In addition, in Lake Erie, an independent and differently oriented sampling program covering 56 stations, including the above 25 stations, was carried out, in which samples from 1 and 5 m, and deeper stations, were obtained. The results of the latter sampling program will be reported separately. In this paper, however, distribution maps from Lake Erie are based on the 1-m depth and 56-station grid. These results have additionally been used for two purposes: a) for statistical analyses of the mixed samples against the 1- and 5-m samples, respectively, and b) for a comparison of the distribution patterns obtained from the 56 and 25 station grid, to evaluate the degree of resolution attainable from the reduced program.

The statistical analyses have shown that the combined errors including repeated sampling, mixing, storage, and processing from the surface layers of a productive lake like Lake Erie are higher than from repeated deep strata sampling of a low productive lake (Strachan 1974).

With regard to the resolution it was found that, of course the resolution obtained from the 25 station grid was less than that of the 56 station grid but the general distribution patterns obtained by the two different sampling grids were essentially the same for all the factors analyzed over the 10 cruises in Lake Erie. Therefore it can be concluded that the biological patterns for Lake Erie based on the 25 station grid only as well as the biological and chemical patterns reported for Lake Ontario (based on 32 stations) are correct in principal.

Basic Features of Heating and Cooling in Lakes Ontario and Erie

The first two Lake Ontario cruises (February and March) fall within the phase of the winter cooling. Temperatures at the beginning of March were lowest and close to 1 C. The temperature distribution during this period was almost uniform over the whole lake, and represented the closest situation to complete mixing of the epilimnetic water masses, except in the northeastern basin which was covered by ice during February and early March. The onset of the thermal bar began in early April and reached its maximal differentiation toward the end of May. The onset of summer stratification over the whole lake developed during June. This first appeared as a horizontal pattern of warmer and cooler water masses. Maximum summer stratification was reached toward the middle of August with an average temperature of approximately 20 C, but with a well-defined north-to-south differentiation with highest values around 24 C at the south shore. A rapid cooling of the epilimnetic waters began during September, with a decrease of the apparent cooling rate during October, which was followed by a continuing regression to lower temperatures in November and December.

In contrast to Lake Ontario, the first cruise in early April in Lake Erie indicated a situation of

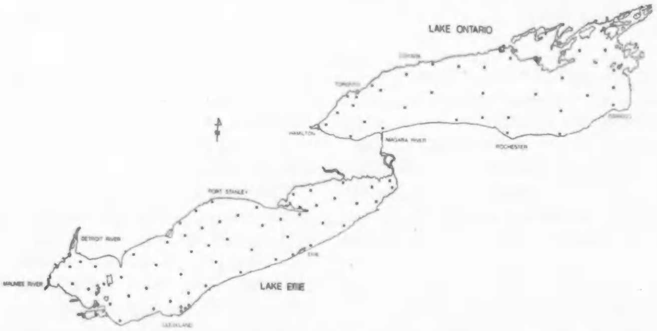


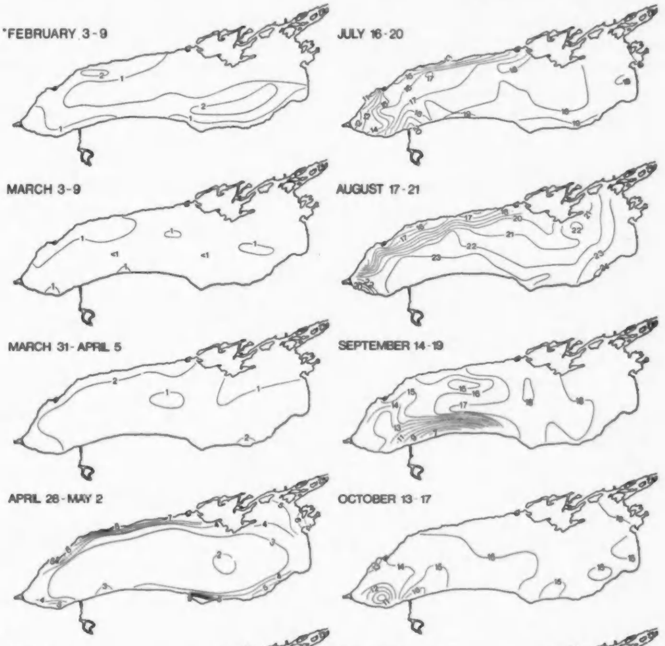
FIG. 1. Location of sampling stations on lakes Ontario and Erie.

moderate horizontal differentiation of the surface temperature. From the distribution pattern, one could define this phase as the onset of a thermal bar, but it was obvious from the following May cruise that this phenomenon, which very strongly develops in Lake Ontario, was much less pronounced in Lake Erie, and could be identified clearly only in the deep eastern part.

During the following months, the heating process of the epilimnetic waters of Lake Erie, in contrast to Lake Ontario, proceeded more rapidly and at the beginning of June the lake was moderately stratified.

The summer stratification, the extent of which, with depth, cannot be defined solely on the basis of surface temperature maps, occurred near the end of August with average temperatures at least 2–3 C higher than in Lake Ontario. Even in late September, surface temperatures still remained close to summer values. After this period, the cooling of the lake proceeded rapidly, producing comparable temperatures to Lake Ontario in October, and by November and December lower ones than those of Lake Ontario.

The difference in behavior of lakes Ontario and Erie, relative to the thermal bar development,



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JULY 16-20

AUGUST 17-21

SEPTEMBER 14-19

OCTOBER 13-17

NOVEMBER 16-20

DECEMBER 7-12

FIG. 2. Temperature distribution patterns in Lake Ontario surface waters, February–December, 1970.

has been mentioned. In addition, in Lake Ontario from June to August, temperatures were considerably lower along the northern–northwestern side than the southern side. This was related to upwelling of cold water along the northern shore. However, in September, a pronounced upwelling occurred

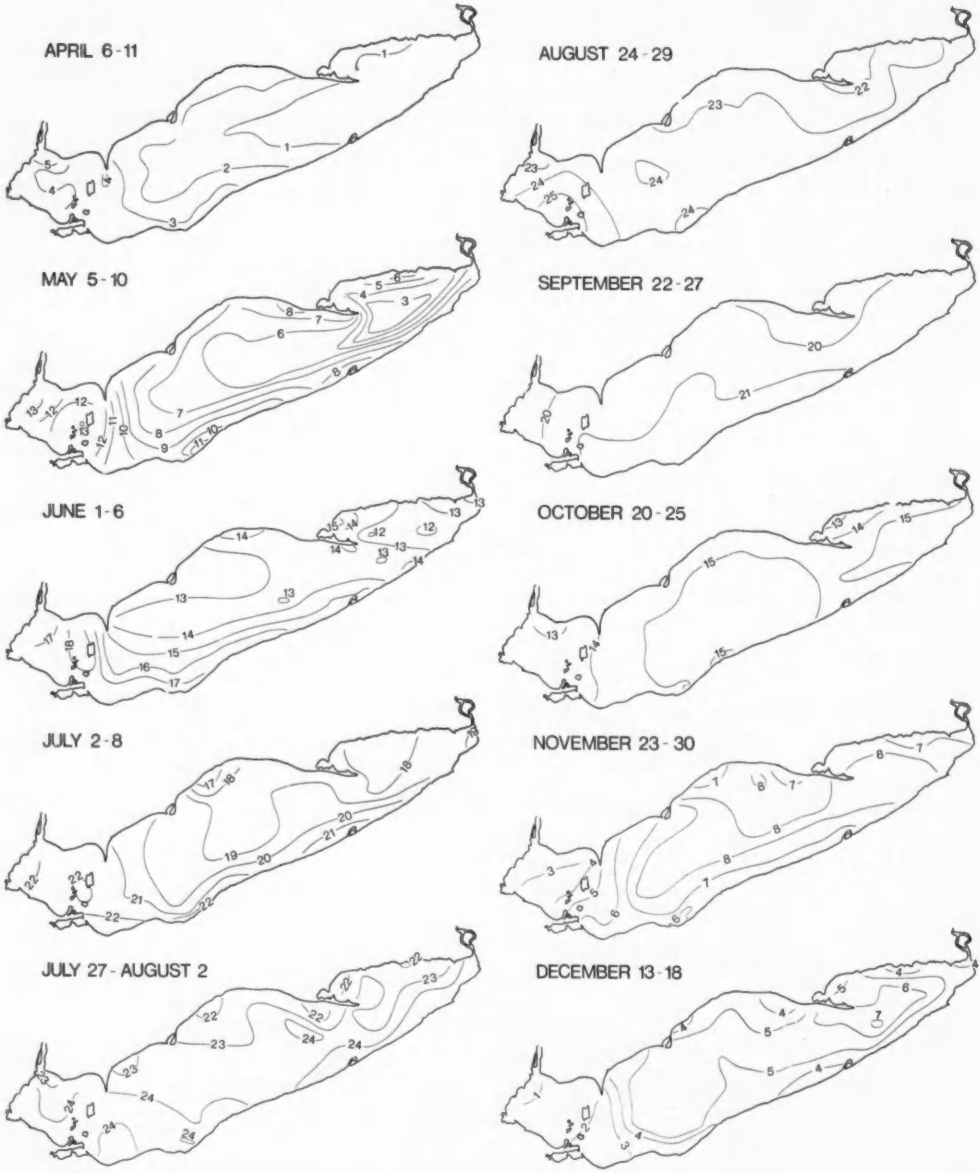
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FIG. 3. Temperature distribution patterns in Lake Erie surface waters, April–December, 1970.

at the southern side of the lake, producing a clockwise displacement of warmer water along the Toronto–Oshawa area.

The unique temperature pattern encountered in June in Lake Ontario represented a complex transition situation between the thermal bar phase and the phase of summer stratification. The complexity of this pattern showed up also in some chemical distribution patterns but had its highest effect on biological processes (Glooschenko et al. 1974b). A similar though less pronounced transition pattern could also be recognized in November. It appeared as a mass of cold water in the eastern part of the central region of the lake, and was probably due to internal waves rather than enhanced cooling.

In central Lake Erie from May until the end of August, temperatures were slightly higher at the southern shore than the northern shore. A second clear temperature gradient occurred in an east-to-west direction from April to July, with highest surface temperatures in the shallow Western Basin and lowest values in the deep Eastern Basin. During fall, the opposite occurred — faster cooling in the Western Basin than in the Central and Eastern basins, resulting in a surface temperature gradient in the opposite direction.

Nutrients in Lakes Ontario and Erie

Total phosphorus (*TP*) — Even in Lake Ontario at the end of the winter mixing, no even distribution of total P was attained (Fig. 4). From February to March, persistent higher TP values prevailed inshore except in the north–northeast. Subsequently,

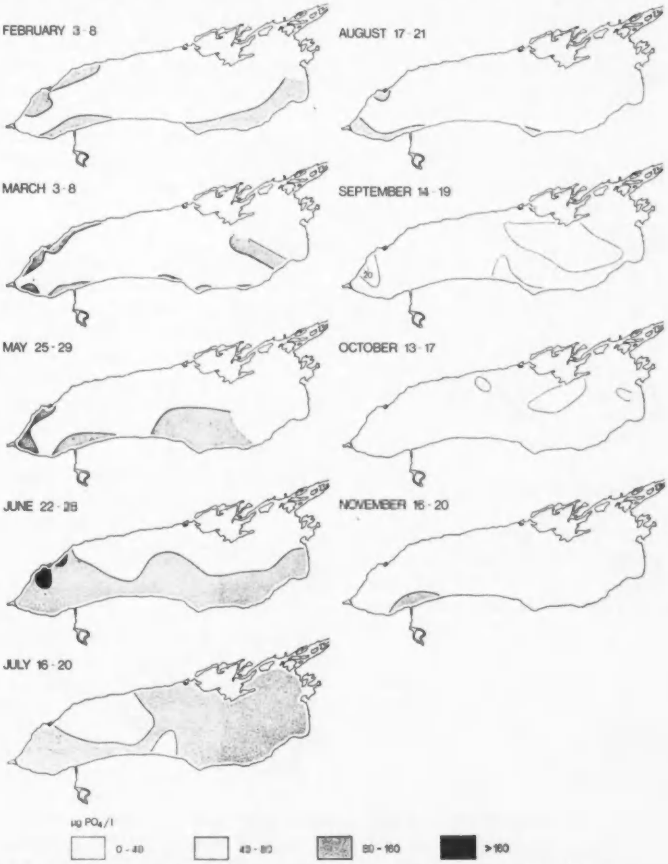


FIG. 4. Horizontal distribution of total phosphorus in Lake Ontario surface waters. Mean concentrations of 1-m and 5-m samples.

instead of a decrease as expected from the onset of the algal production cycle, total phosphorus continued to increase, particularly in the south, and reached its maximum in June in the Toronto area, (>200 µg PO_4/liter). This period of continuous increase at the surface layer was followed by a period of TP loss due to sedimentation, which became most pronounced in the eastern region. From September to November, a slight lakewide increase of TP concentration in the surface layer was observed.

The total phosphorus distribution patterns in Lake Erie (Fig. 5) showed a clear west–east gradient with highest concentrations in the Western Basin, and increasing concentrations in a southerly direction in the Central Basin.

In the Western Basin phosphorus concentrations were normally higher than 80 µg PO_4/liter and often varied in the southern half between 100 and 200 µg PO_4/liter; the highest value observed was 450 µg PO_4/liter. Although the Detroit River is the main phosphorus source of Lake Erie and its mean concentration of total phosphorus ranges around 300 µg PO_4/liter (International Joint Commission Report 1969), the concentration at the nearest station to the inlet never exceeded 315 µg PO_4/liter, and from May to October was below 80 µg PO_4/liter. Therefore, either a large part of the total phosphorus

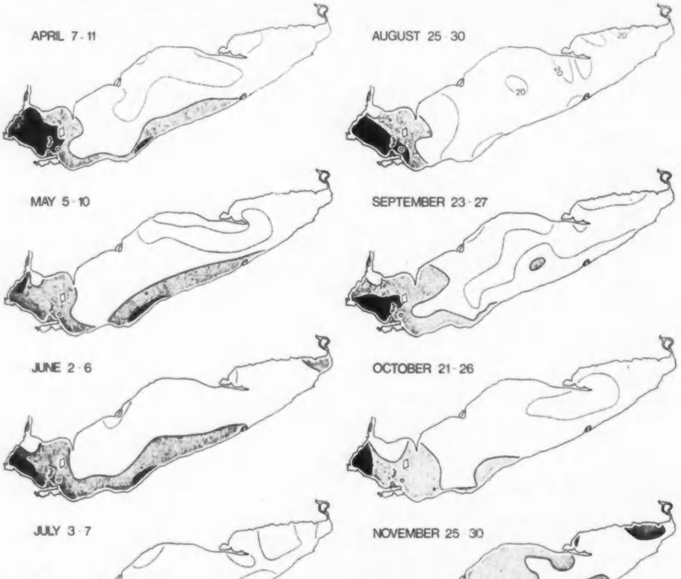


FIG. 5. Horizontal distribution of total phosphorus in Lake Erie surface waters (1 m).

entering the lake by the Detroit River becomes sedimentated immediately near the inlet, or the data presented in Fig. 8, collected from only six stations in western Lake Erie, do not show the true picture of the spatial phosphorus distribution in this basin. Flow from the river tends to be concentrated inshore and is missed at the station. Often concentrations in the southwestern part of the basin were higher than in the northern half, probably due to discharge from the nutrient-rich Maumee River (IJC 1969).

In the Central and Eastern basins, total phosphorus concentration increased slightly from April to June. From then until September, losses of total phosphorus by sedimentation were higher than the phosphorus supply to the lake surface. At the southern shore concentrations were always higher than in the open lake or along the northern shoreline, and this was consistent with other nutrients, reflecting the discharge of sewage from Cleveland and Erie, Pa. The latter city is characterized by a nearshore peak in algae (Glooschenko et al. 1974b). With decreasing temperature in September, the total phosphorus concentration began to increase again inshore, resulting in highest concentrations in the Western Basin and lowest in the Eastern Basin.

Soluble reactive phosphorus (*SRP*) — Soluble reactive phosphorus in Lake Ontario, in contrast to TP, exhibited an essentially different cycle showing variations from more than 100 to less than 5 μg PO_4/liter. In February, two regions of relatively high SRP concentrations were observed, one along the north–northwestern shore and the other in the southeast (Fig. 6). However, in March, SRP concentrations had started to decrease along the shore, with the exception of the Toronto region, but increased slightly over 40 μg PO_4/liter in the deep region of the lake. At the end of April and throughout May, a well-defined distribution pattern of SRP evolved which resembled that of the thermal bar but which essentially was related to the onset of the production cycle inside the bar (Glooschenko et al. 1974a; Munawar and Nauwerck 1971). The SRP decrease was more pronounced along the eastern than the southern shore. The June pattern, though reflecting a further progression of the previous phase, was also related to the complex thermal transition pattern. In addition, as seen from the nitrogen and silica patterns, upwelling in the Toronto region appeared to cause increased SRP. In the eastern part of the lake, the SRP concentrations were very low, less than 5 μg PO_4/liter. By mid-July the area showing values below 5 μg PO_4/liter extended over almost the whole lake, with the exception of the Toronto–Hamilton–Niagara region. In August and September, the area with concentrations higher than 5 μg PO_4/liter extended along the southern shore in an easterly direction. In September, the high values on the southern shore were at least due in part to the upwelling of hypolimnetic waters, and in addition one recognized the clockwise displacement of such waters toward the Toronto–Oshawa area.

During the decrease of cooling rate in October, the whole lake surface again became almost entirely depleted of SRP, but in November–December the SRP concentrations began to increase. The November cruise covered a complex situation with low concentrations in the central part and higher values at the western and eastern ends of the lake. The SRP distribution in December showed a correspondence with the temperature distribution, with higher phosphorus concentrations in the western low temperature area; however, the concentrations reached only about half the values observed on the previous February cruise.

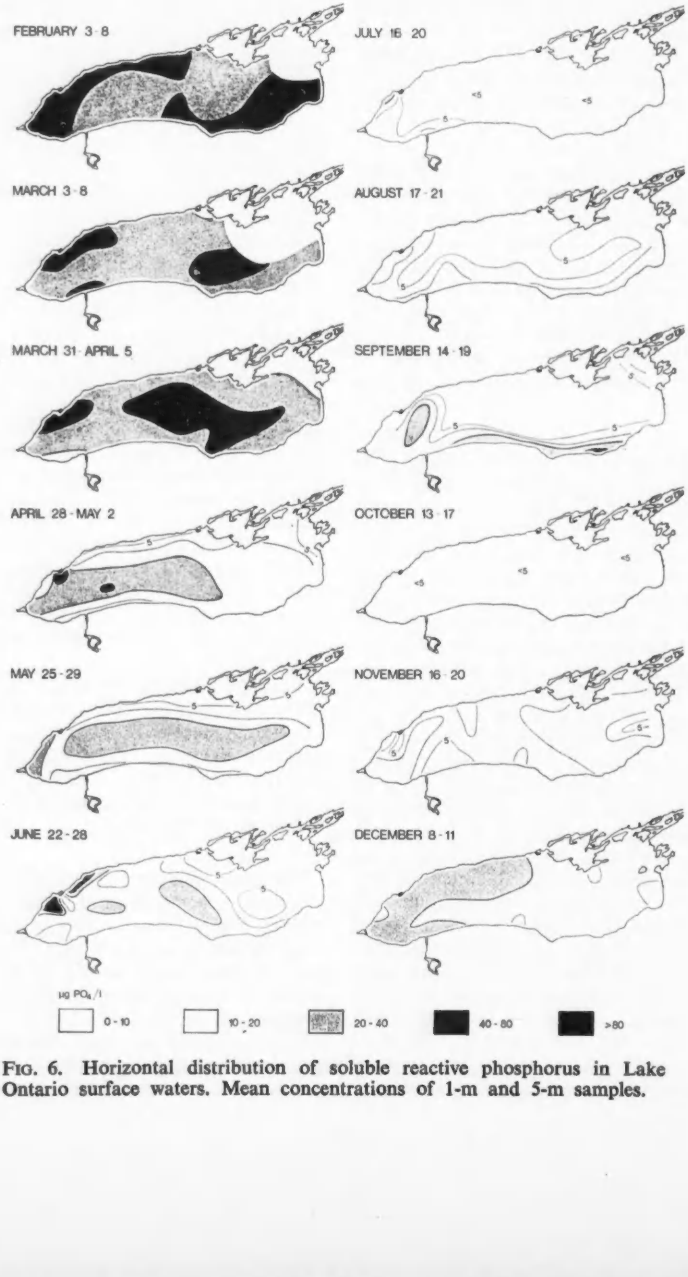
Distribution patterns of SRP in Lake Erie differed in several respects from those in Lake Ontario (Fig. 7). In Lake Ontario, SRP began to decrease along the shore as late as April. Apart from the high concentrations along the southern shore, SRP was very low in the Eastern and Central basins of Lake Erie, probably due to early onset of the spring algal peak (Glooschenko et al. 1974b). In July and August, SRP became almost completely depleted, even along the southern shore which showed fairly uniform values in the Central and Eastern basins, with concentrations below or slightly higher than 5 μg PO_4/liter. With the cooling in October, SRP concentrations increased rapidly lake-wide and reached their highest values in November.

Within the shallow Western Basin, it was hard to detect a clear, seasonal trend. The highest values for soluble reactive phosphorus were usually found in the southern half of the basin. The highest value observed was 120 μg PO_4/liter in April, but a month later concentrations had decreased to values below 10 μg PO_4/liter.

Inorganic nitrogen — The concentrations of total inorganic nitrogen (sum of nitrate, nitrite, and ammonia) varied from more than 300 to less than 5 μg N/liter in Lake Ontario. From a qualitative point of view, spatial and temporal variations were similar to those of SRP (Fig. 8). Over the first 2 mo, nitrogen remained fairly evenly distributed over the whole basin. In April concentrations started to decrease along the northern shore and on the southern shore west of the Niagara River discharge.

Contrary to SRP and the silica concentrations (see below) which showed complementary similarities to the surface temperature structure, the nitrogen distribution did not show lower concentrations along the entire lakeshore perimeter even in May.

The decrease of nitrogen concentration was most pronounced from May to the end of June, when it decreased in most areas of the southern half of the lake to concentrations below 50 µg N/liter. Higher concentrations always occurred along the shores where upwelling was present. Similar to the distribution of SRP, concentrations were always slightly higher along the southern than along the northern shore from July to September. As for SRP, a first minimum of N concentration was observed in July and a second in October. From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5
DECEMBER 8-11
µg PO₄/l
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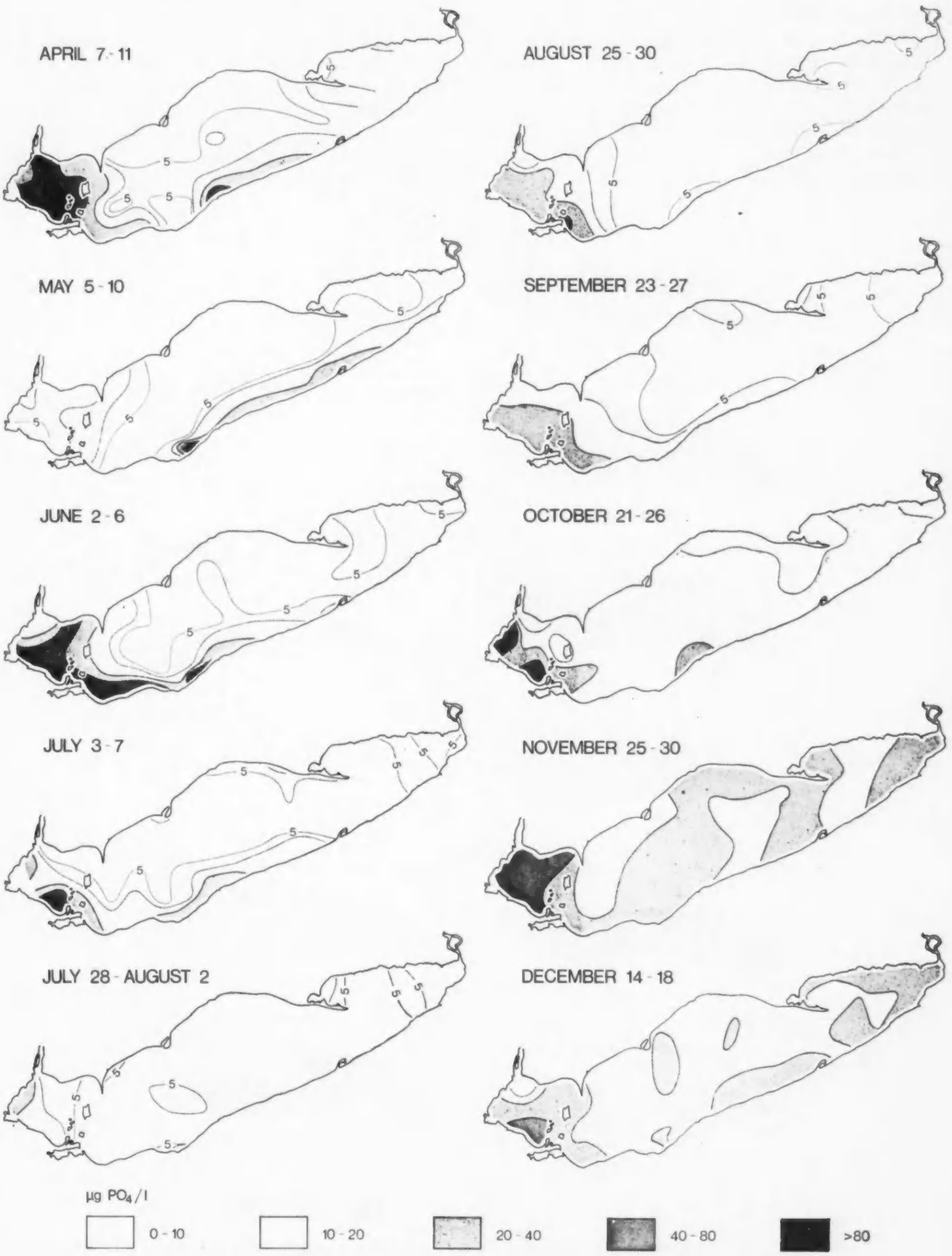
10-20
20-40
40-80
>80

FIG. 6. Horizontal distribution of soluble reactive phosphorus in Lake Ontario surface waters. Mean concentrations of 1-m and 5-m samples.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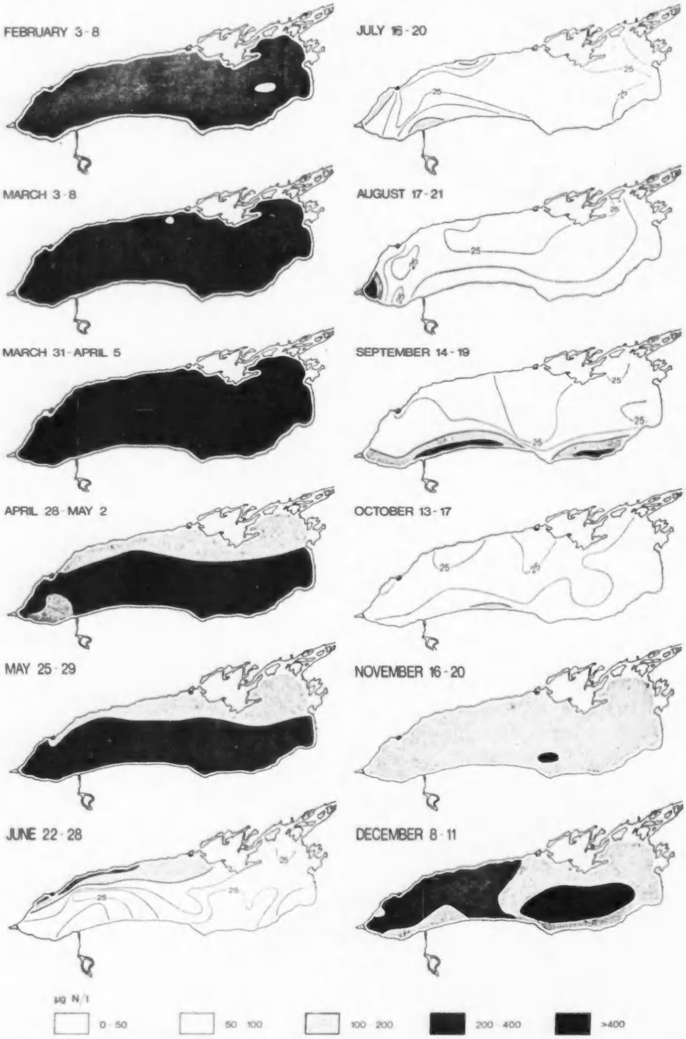
OCTOBER 21 - 26
NOVEMBER 25 - 30
DECEMBER 14 - 18
µg PO4 / l
0 - 10
10 - 20
20 - 40
40 - 80
>80

FIG. 7. Horizontal distribution of soluble reactive phosphorus in Lake Erie surface waters (1 m).

then to December, concentrations increased continuously to almost the same level observed during the previous February cruise.

In Lake Erie, to July, the pattern of inorganic nitrogen was consistent and similar to total phosphorus and SRP patterns, with concentration gradients in the west–east and south–north direction as mentioned (Fig. 9).

On the April cruise, a zone of relatively low concentration of inorganic nitrogen was detected along the northern shore and at some pelagic stations between Port Stanley, Ont. and Cleveland, Ohio. This tongue of low concentration extended in an east–west direction in April and May. Until September 23–27, in the Central and Eastern basins, nitrogen concentrations had decreased at most of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µg N/l
0 - 50
50 - 100
100 - 200
200 - 400
>400

FIG. 8. Horizontal distribution of total inorganic nitrogen ($NO_3 + NO_2 + NH_4$) in Lake Ontario surface waters. Mean concentrations of 1-m and 5-m samples.

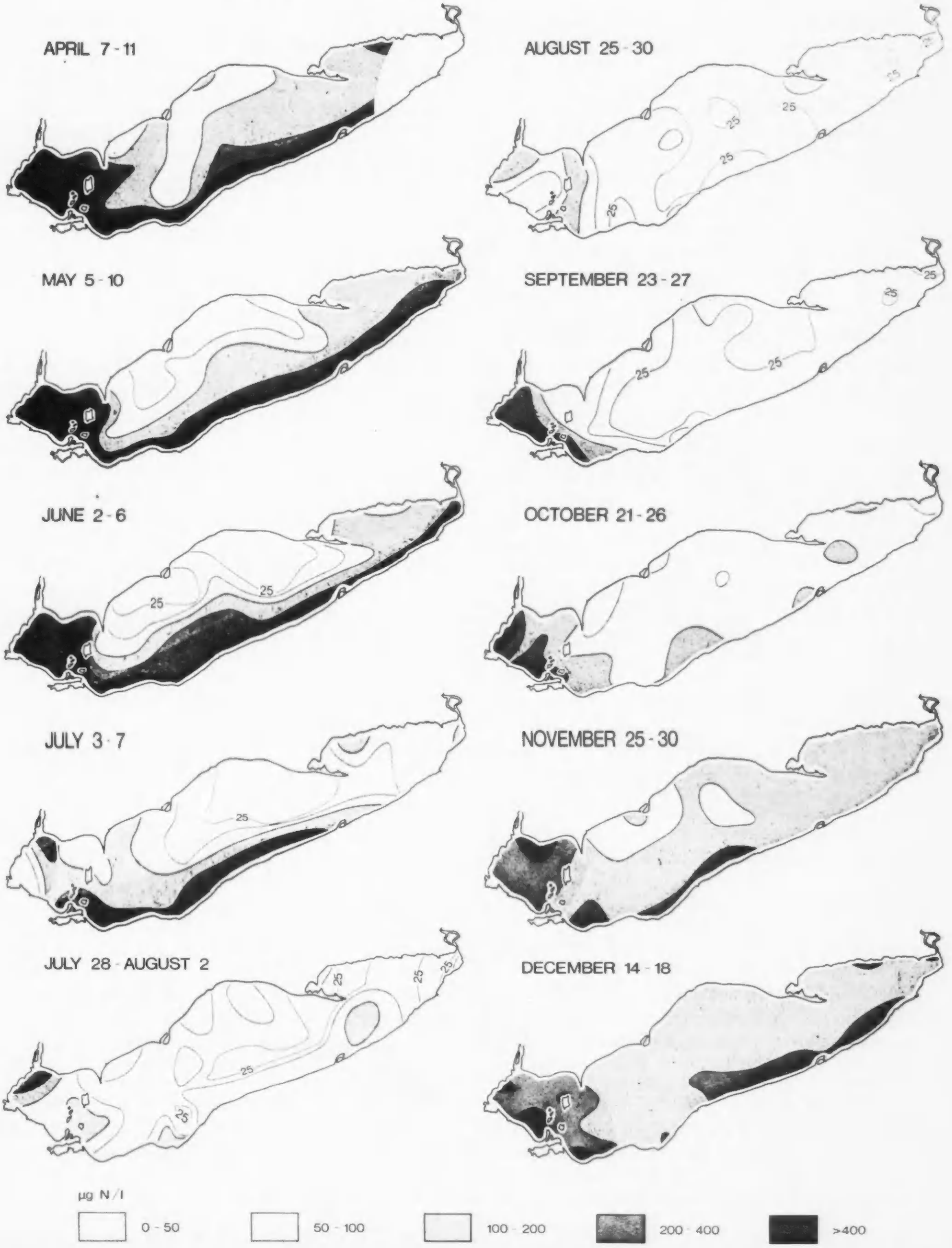

APRIL 7 - 11
AUGUST 25 - 30
25
MAY 5 - 10
SEPTEMBER 23 - 27
25
JUNE 2 - 6
25
OCTOBER 21 - 26
JULY 3 - 7
25
NOVEMBER 25 - 30
JULY 28 - AUGUST 2
25
DECEMBER 14 - 18
µg N / l
0 - 50
50 - 100
100 - 200
200 - 400
>400

FIG. 9. Horizontal distribution of total inorganic nitrogen ($NO_3 + NO_2 + NH_4$) in Lake Erie surface waters (1 m).

the stations to values below 25 μg N/liter. In October they began to increase lake-wide, resulting in a similar pattern as spring concentrations.

Soluble reactive silicate (*SRS*) — The distribution of SRS in Lake Ontario (Fig. 10) showed higher concentrations in the western than in the eastern half of the lake from February to the beginning of April. Until the end of May, this pattern evolved progressively, becoming similar to those discussed for SRP, and in fact, was closely related to spring development of major diatom populations (Munawar and Nauwerck 1971). The lowest overall concentrations with less than 100 μg SiO_2/liter were observed in July, but in the preceding month large areas of the lake were depleted to less than 100 μg SiO_2/liter.

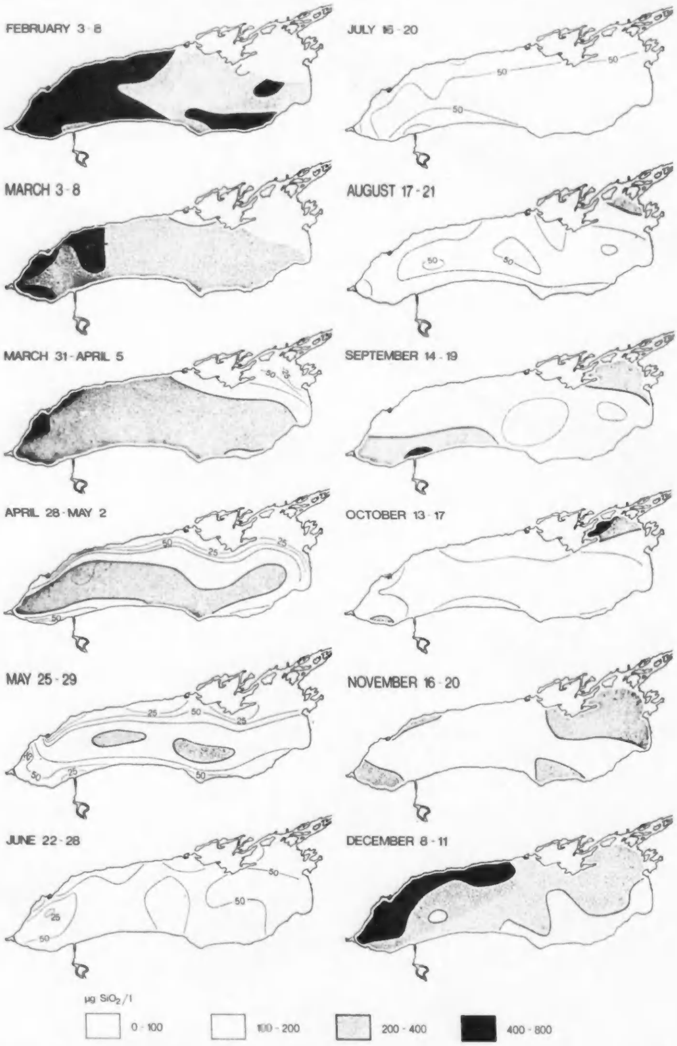

FEBRUARY 3-8
MARCH 3-8
MARCH 31-APRIL 5
APRIL 28-MAY 2
MAY 25-29
JUNE 22-28
JULY 16-20
AUGUST 17-21
SEPTEMBER 14-19
OCTOBER 13-17
NOVEMBER 16-20
DECEMBER 8-11
50
25
μg SiO2/l
0-100
100-200
200-400
400-800

FIG. 10. Horizontal distribution of soluble reactive silica in Lake Ontario surface waters. Mean concentrations of 1-m and 5-m samples.

Slightly faster than SRP, SiO_2 started to regenerate in August and September from the shore to the center. In October, the SRS concentrations reached a second minimum in the seasonal cycle, probably due to the fall increase of diatoms. From then until December, concentrations increased progressively lake-wide, resulting in higher concentrations along the northwestern shore, then along the southeastern shore, similar to the regeneration of SRP.

In contrast to Lake Ontario, changes in concentrations of soluble reactive phosphorus and silicate in Lake Erie appeared to be unsynchronized (Fig. 7 and 11). In the Central and Eastern basins, SRS was low at the beginning of April. In the second part of May, concentrations had started to increase at the northern as well as the southern shore, reaching a maximum at the end of August, when SRP concentrations reached minimum values. In the Central Basin, SRS decreased a second time during September and October when N and P concentrations had started to increase. Highest values were observed in mid-December when concentrations were about 10 times as high as the preceding April.

In the Western Basin, SRS concentrations were still very high in April but decreased in the magnitude of 1000 µg SiO_2/liter between April and May. To the end of July, concentrations increased. Two secondary minima were observed during August and November. Whereas in the Central and Eastern basins of Lake Erie, and in Lake Ontario, the SiO_2 concentrations never exceeded values of 800 µg SiO_2/liter, this concentration was exceeded in western Lake Erie quite often.

Nutrient-Phytoplankton Relationships in Lakes Ontario and Erie

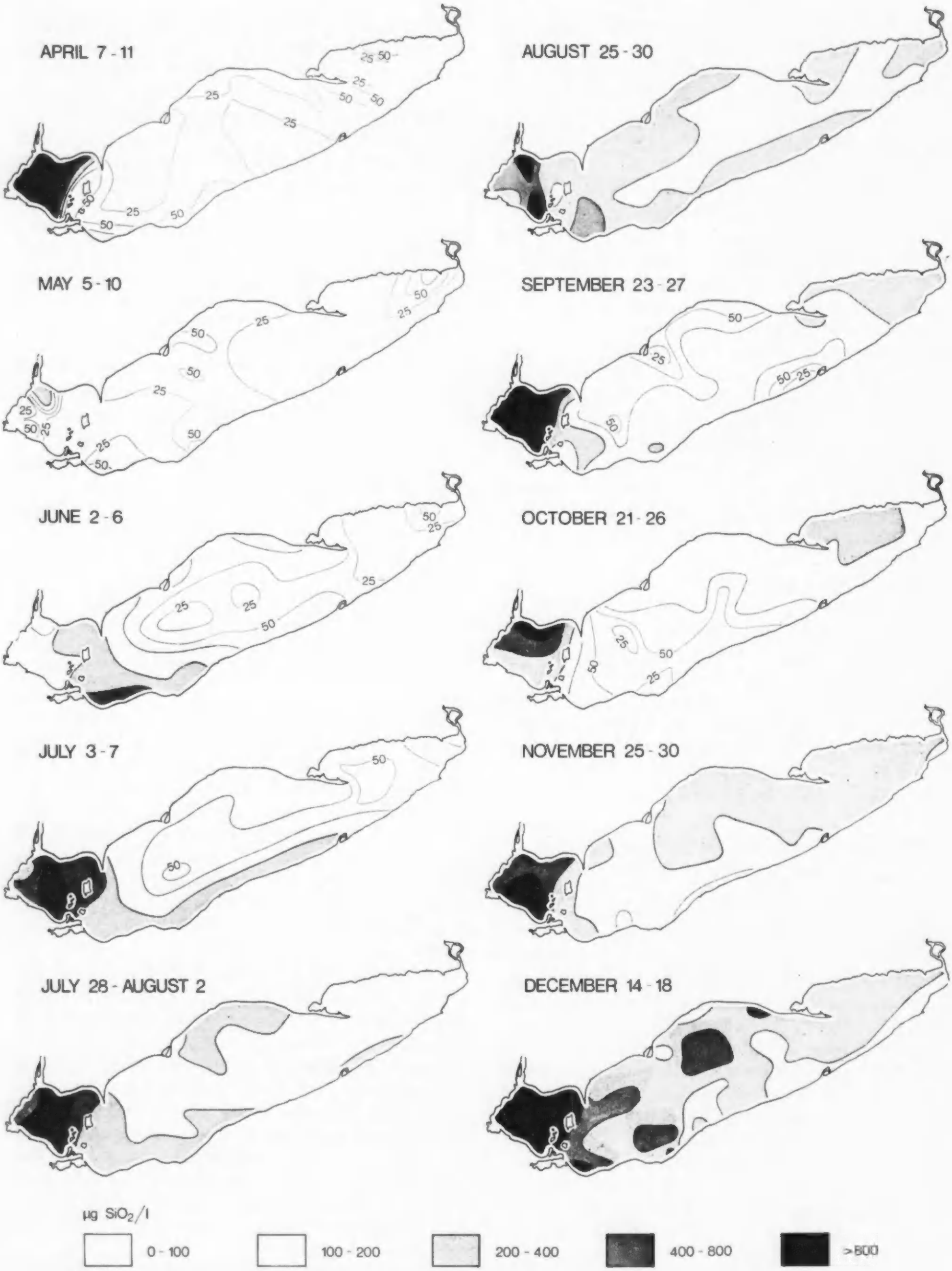
The surface pattern of dissolved inorganic nutrients is the result of nutrient supply, regeneration, and net assimilation of nutrients by algae. There are some essential differences in the chemical-biological behavior of the two lakes, which need further discussion. In Lake Erie the nutrient concentrations were much lower in April and the onset of a sharp nutrient concentration decrease must have started much earlier in the year than in Lake Ontario. To explain this different behavior, it must be mentioned that the net uptake of SRP, inorganic nitrogen, and SRS is related to net photosynthesis and therefore depends not only on the nutrient concentration and the solar radiation, but also on the depth of the mixed layer (Sverdrup 1953; Vollenweider 1970; Talling 1971). The thicker the mixed layer is in relation to the trophogenic depth, the lower becomes the ratio between photosynthesis and respiration. Net photosynthesis and therefore nutrient uptake in general can become zero or even negative when mixing depth is large enough. Since central and eastern Lake Erie are much shallower (mean depth 18 m and 26 m, respectively) than Lake Ontario (mean depth 84 m), this would explain why the onset of the spring algal bloom, and, therefore, the decrease of inorganic nutrients, starts much earlier in spring in Lake Erie than in Lake Ontario. In both western and central Lake Erie, the phytoplankton spring bloom had probably passed its maximum before the first cruise in early April (Glooschenko et al. 1972b, 1974a, b). At this time in central Lake Erie, chlorophyll *a* values were higher than 4 µg/liter in more than two thirds of the lake surface area, whereas in Lake Ontario (March 31–April 5), this value was attained or slightly exceeded only in the shallow northeastern part and in a narrow band along the shore.

Besides this different behavior with regard to the onset of the spring bloom in the two lakes, their nutrient patterns are also qualitatively clearly different in April and May. In Lake Ontario during spring, zones with high chlorophyll concentration and high production rates coincided with areas low in nutrient concentration, and vice versa. In Lake Erie just the opposite was found. Chlorophyll *a* and the production distribution showed a direct similarity to the nutrient pattern in Lake Erie at this time.

The circular inshore–offshore patterns observed in Lake Ontario during the thermal bar buildup can be explained by different mixing properties of inshore and offshore waters. Inside the thermal bar the water masses were stratified, but not in the central part of the lake where surface temperatures were still close to 4 C. The lower nutrient concentrations along the shore must therefore be interpreted as the result of an increased net uptake rate by phytoplankton due to the shallower mixing depth.

In Lake Erie the phenomenon of the thermal bar was less pronounced than in Lake Ontario. During the periods May 1–10 and June 1–6, production was highest in the warmwater areas of western Lake Erie and the southern shore, but this increased production did not result in lower nutrient concentrations. Yet, the cause of the high nutrient concentration was not a slower net uptake rate, but could be caused by nutrient discharge from the main nutrient sources: the Detroit and Maumee rivers in the Western Basin and municipal discharges from Cleveland and Erie on the southern shore of the lake.

From June to the end of August, in Lake Erie (Central and Eastern basins), the N and P concen-


APRIL 7 - 11
AUGUST 25 - 30
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OCTOBER 21 - 26
JULY 3 - 7
NOVEMBER 25 - 30
JULY 28 - AUGUST 2
DECEMBER 14 - 18
25
50
µg SiO₂/l
0 - 100
100 - 200
200 - 400
400 - 800
>800

FIG. 11. Horizontal distribution of soluble reactive silica in Lake Erie surface waters (1 m).

trations decreased at all locations to values of about 25 µg N/liter and less than 5 µg PO_4/liter, but the distribution of chlorophyll *a* and primary production still showed the typical pattern with highest values along the southern shore. In Lake Ontario in offshore regions, the N and SRP concentrations decreased to about the same values, but along the northwestern and southern shores they were always slightly but significantly higher. This suggested that in Lake Erie the phytoplankton during this period was capable of immediately assimilating the entire nutrient supply, whereas in Lake Ontario in the Toronto–Hamilton region and along the southern shore, this did not appear to be the case. In this region, upwelling occurred frequently. The chlorophyll distribution and the primary production pattern in June and September showed that in upwelling zones, biomass concentration and primary production decreased. The main reason for this might be the low concentration of living algae in the upwelled hypolimnic water, but in addition one assumes that any single event of upwelling occurs in too short a time period to allow the buildup of a higher algal biomass.

In October, a second nutrient concentration minimum was observed in all Lake Ontario, but in Lake Erie, the concentrations of inorganic nitrogen and SRP had started to increase. This different behavior has to be explained by an earlier onset of fall overturn in Lake Erie but not by a lower nutrient uptake rate, since primary production was still higher in Lake Erie (120 mg C/m^2 per hour) than in Lake Ontario (80 mg C/m^2 per hour) at this time (Glooschenko et al. 1974a). With the exception of the deepest eastern part of Lake Erie, the vertical temperature distribution was nearly isothermal (temperature difference throughout the water column was less than 0.2 C) at this time of year. However, in Lake Ontario, temperature was normally below 5 C at depths greater than 50 m, which, when compared with the surface temperature pattern (Fig. 2), shows that most of Lake Ontario was still well stratified at this time.

To sum up, Lake Erie and Lake Ontario differed in their seasonal nutrient cycle. In Lake Erie, nutrient concentrations started to decrease much earlier in the spring. In Lake Ontario in April and May, due to the influence of stratification on the shoreside of the thermal bar, the buildup of algal biomass led to low nutrient concentrations along the entire shore. In Lake Erie the nitrogen and phosphorus distribution pattern showed the highest concentrations along the southern shore, due to the high nutrient supply of municipalities such as Cleveland and Erie. In July, August, and September, inorganic nitrogen and SRP became almost completely depleted lake-wide in Lake Erie, but in Lake Ontario concentrations increased slightly in the Toronto–Hamilton area and along the southern shore, due to the combined effect of external nutrient discharge from municipalities and upwelling. Finally, in Lake Erie, the nutrient concentrations started to increase in October due to fall overturn, whereas in Lake Ontario, a second nutrient minimum was observed at this time due to the fall buildup of phytoplankton.

Acknowledgments

We wish to thank Dr V. Chawla, who at the time was responsible for the supervision of the analytical group of the Water Quality Detachment of the CCIW, and Mr H. H. Dobson who prepared the distribution maps. R. Gächter acknowledges a postdoctoral fellowship granted by the National Research Council of Canada.

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In Situ Measurement of the Settling Velocity Profile of Particulate Organic Carbon in Lake Ontario

N. M. Burns and A. E. Pashley

Descriptive Limnology Section
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

Burns, N. M., and A. E. Pashley. 1974. In situ measurement of the settling velocity profile of particulate organic carbon in Lake Ontario. J. Fish. Res. Board Can. 31: 291–297.

Depth profiles of calm water settling velocities were measured in situ using specially constructed sampling bottles. Samples of water were taken at specific depths and the settling process commenced as soon as the samples were taken. Just before retrieval of the bottles, the samples were subdivided into upper and lower portions so that settling velocities could be calculated; these varied between –0.4 and +2.0 m day^{-1}. Net settling velocities measured at the top of the thermocline were used to estimate net settling fluxes from the epilimnion; these varied between –0.074 and +0.336 mmoles of phosphorus $\text{m}^{-2}\ \text{day}^{-1}$. Net settling flux can differ from sedimentation flux out of the epilimnion and the necessity for a clear distinction between these two values is emphasized.

Burns, N. M., and A. E. Pashley. 1974. In situ measurement of the settling velocity profile of particulate organic carbon in Lake Ontario. J. Fish. Res. Board Can. 31: 291–297.

A l'aide de bouteilles d'échantillonnage spécialement construites, les auteurs ont établi des profiles bathymétriques de vitesses de sédimentation en eau calme. Ils ont recueilli dans ces bouteilles des échantillons d'eau à des profondeurs déterminées, le processus de sédimentation commençant aussitôt l'échantillon prélevé. Juste avant le recouvrement des bouteilles, les échantillons sont subdivisés en portions supérieure et inférieure, de façon à permettre le calcul des vitesses de sédimentation. Ces vitesses varient de –0.4 à +2.0 m jour^{-1}. Les vitesses nettes de sédimentation à la partie supérieure de la thermocline ont été utilisées pour estimer les flux de sédimentation en provenance de l'épilimnion, et ces derniers varient de –0.074 à +0.336 mmoles de phosphore $\text{m}^{-2}\ \text{jour}^{-1}$. Le flux net de sédimentation peut être très différent du flux de sédimentation hors de l'épilimnion, et les auteurs insistent sur la nécessité d'une distinction précise entre ces deux valeurs.

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The problem of phytoplankton settling has been reviewed by Smayda (1970). The results of many laboratory investigations (Riley 1943; Lund 1959; Steele and Yentsch 1960; Smayda and Boleyn 1965; Eppley et al. 1967), show that the observed settling velocities depended on the species under consideration that in turn depended on prevailing light conditions, cell concentrations, growth rate, nutrient concentrations, and the physiological state of the cells. To predict the settling velocity of a species under natural conditions, the above factors would have to be considered along with the effects of zooplankton grazing and the density stratification in the natural water body. Considering our present state of knowledge, it is impossible to predict the settling velocities of natural phytoplankton populations on the basis of laboratory studies.

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In addition, it is necessary to measure net settling fluxes that are the result of simultaneous upward and downward fluxes. This would rule out the use of sedimentation traps. With these requirements in mind the in situ settling velocity bottle was developed.

Materials and Methods

THE IN SITU SETTLING VELOCITY BOTTLE

The settling velocity bottle consists of a 1-m long plastic cylinder that has a cross-sectional area of approximately 100 cm^2 and is closed with rubber end plugs and an actuating mechanism from a standard Van Dorn bottle (Fig. 1). At a distance of 66 cm below the top of the bottle is a sealed box which is an integral part of the sampling bottle. Inside the box is a flat, horizontal shutter, which can slide across the sampling bottle to divide it in two. The whole unit is watertight

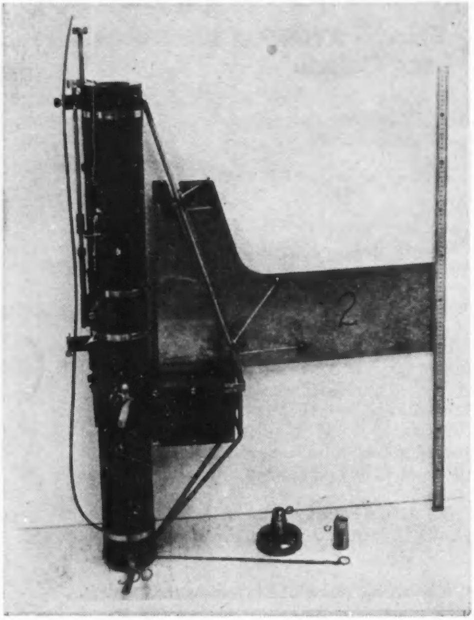


FIG. 1. The in situ settling velocity bottle.

but there is the possibility of slight mixing of the water in the upper and lower sections with the water in the shutter box. The shutter can be pulled back against a spring to automatically engage with a trigger mechanism which then holds the shutter in the open, cocked position. Each bottle has two triggers and when a small diameter messenger is dropped, it strikes the trigger closest to the mooring cable which causes the end caps to close the bottle. When a large diameter messenger is dropped, it strikes the second trigger which causes the shutter to segment the bottle into two compartments. Attached to the outside of the bottle is a vane assembly which together with a special swivel clamp, enables the bottle to rotate freely on the taut mooring wire to line up with the current and suffer minimum vibration due to vortex-shedding.

A taut wire-mooring (Fig. 2) ensures that the settling velocity bottles move as little as possible. To set the mooring into the water, a capstan and snatch block are used to lower the anchor slowly while each sampling bottle is added to the line together with two mechanical messengers. When the mooring has been set, the lanyard trigger on the surface float is actuated to release the smaller of the two messengers. After approximately 90 min, the lanyard is again pulled releasing the larger messenger.

The complete system is retrieved in the reverse order to its installation. The bottles are immediately drained into separate containers by first opening the valve at the base of the upper section of the sampler. Next, the plug in the shutter box is removed, allowing the water in the shutter box to drain to waste. The lower water column is next drained through a valve at the bottom of the sampler, care being taken to drain out all the collected particulate material.

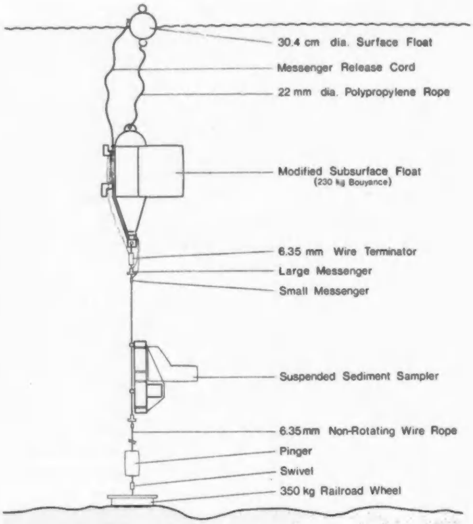

30.4 cm dia. Surface Float
Messenger Release Cord
22 mm dia. Polypropylene Rope
Modified Subsurface Float
(230 kg Bouyance)
6.35 mm Wire Terminator
Large Messenger
Small Messenger
Suspended Sediment Sampler
6.35mm Non-Rotating Wire Rope
Pinger
Swivel
350 kg Railroad Wheel

FIG. 2. The mooring arrangement required for a set of in situ settling velocity bottles.

The water from the top section is split into two portions and each is filtered through a GF/C filter paper and acid washed to dissolve any precipitated carbonates. The same procedure is followed with the water obtained from the lower section of the settling bottle. The concentration of particulate organic carbon (POC) in the upper and lower sections is obtained from combustion of the filter papers in Carbon–Hydrogen–Nitrogen analyzer. The volume of water in the upper and lower sections is measured and these values, with the knowledge of the concentration difference between the upper and lower sections, make it possible to calculate the net settling velocity and net settling flux of the particulate organic carbon.

If f = quantity of POC which settled into the bottom segment of settling velocity bottle, V_t = volume of top segment, C_t = final concentration of POC in top segment, V_b = volume of bottom segment, C_b = final concentration of POC in bottom segment, $d = C_b - C_t$, then the initial concentration of POC in the settling bottle C_i, is given by

$$C_i = (V_t\, C_t + V_b C_b) \,/\, (V_t + V_b) \qquad (1)$$

and the net transport from the top segment of the bottle to the lower segment is given by

$$f = V_b (C_b - C_t) \qquad (2)$$

$$= d\, V_b (V_t / (V_t + V_b) \qquad (3)$$

If F is the net settling flux then

F = *f* / (cross-sectional area) × (settling time). The net settling velocity, S, is given by

$$S = F/C_t, \text{ if } C_t \text{ is approximately equal to } C_t. \qquad (4)$$

The only variable in the righthand side of Eq. (3) is *d* and thus the uncertainty in the flux is determined by the uncertainty in *d*. The standard deviation for the difference between the two measured quantities was calculated according to the method given by Youden (1951).

Divers determined that the subsurface float should be set at approximately 10-m depth to prevent significant disturbance by waves of approximately 1-m height. The bottles were immersed three or four times during an investigation period and with the first cast the top bottle was usually set at 15 m. The remaining five bottles were then set each 10 m deeper than the bottle above. In the next cast the shallowest bottle was set at the depth of the deepest bottle of the previous cast. It was hoped that by means of this procedure, it would be possible to obtain a profile of settling velocities together with some idea of the reproducibility of the results obtained at different times during the day from the same depth.

While on station, profiles of concentration with depth were taken by sampling at a number of depths for POC, particulate phosphorus, and soluble phosphorus. The temperature profile was obtained with an electronic bathythermograph. The phosphorus analyses were carried out by methods described by Philbert and Traversy (1974). The settling velocity of particulate phosphorus at a specific depth was assumed to be the same as the net settling velocity of particulate carbon at the same specific depth and time (Fig. 3). Settling velocity was multiplied by concentration of particulate phosphorus as obtained from the concentration profile data to obtain the settling flux of particulate phosphorus at a specific depth.

The chemical profile data was also used for the calculation of the concentration gradients for total phosphorus. These gradients were then used to calculate the flux through the top of the thermocline into the epilimnion from estimates of the diffusion coefficient based on temperature surveys of Lake Ontario (F. M. Boyce and T. J. Symons, Canada Centre for Inland Waters, Burlington, Ont., personal communication).

Results

The results of four measurements of the settling velocity profile in Lake Ontario are presented in Fig. 3; Fig. 4 shows two successive profiles of the concentration of POC on July 19. The experiments were conducted between 0900 and 2000 h at Station 19 (43°36.0′ N, 78° 1.0′ W), Lake Ontario, approximately midlake from both the east–west and north–south directions.

The contribution of phosphorus to the epilimnion from the thermocline by entrainment of the thermocline into the epilimnion is not considered. Table 1 shows the settling flux calculated at the depth of the top of the thermocline (T.T.) for each of the four investigations.

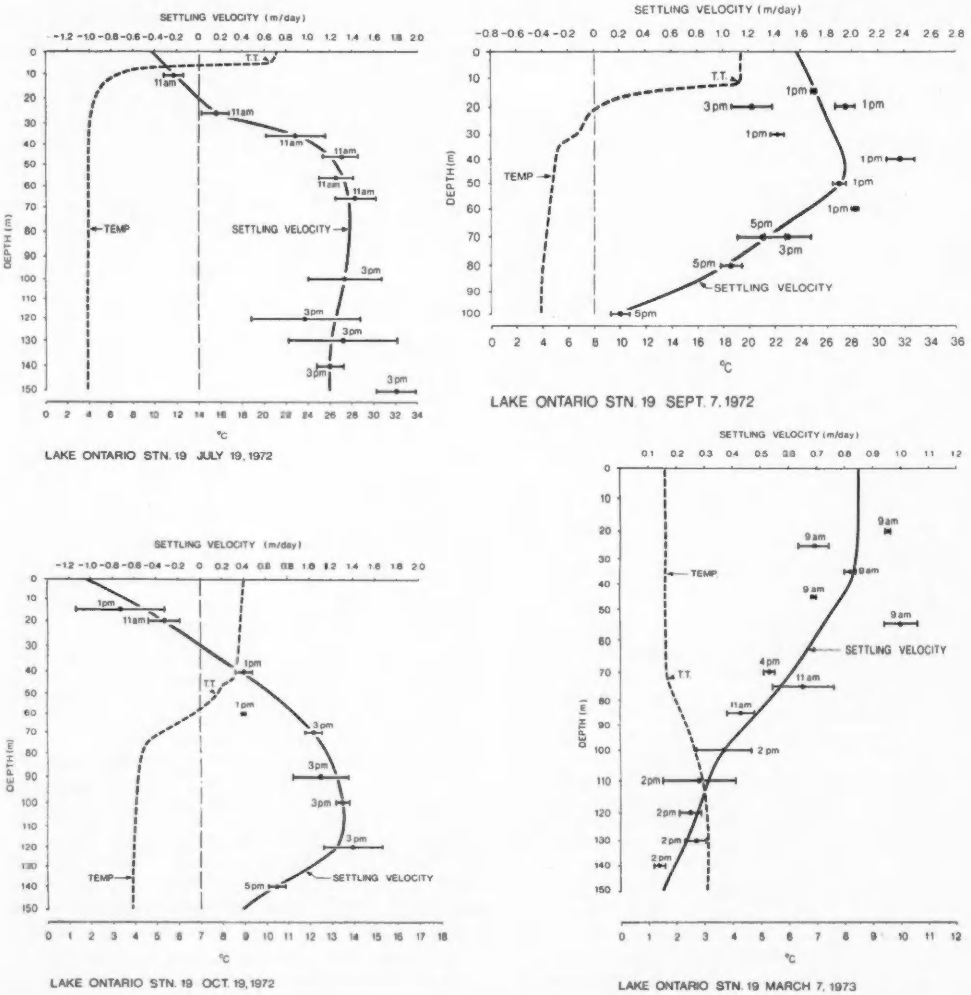
During July and September, the lake had normal summer stratification. It was not possible to estimate the diffusion coefficient for the top of the thermocline during October because the lake was undergoing the transition from summer stratification to fall isothermal conditions. During March 1973, the lake was in a state of winter stratification. On September 7, 1972, the somewhat unusual condition existed when the lowest concentrations of total phosphorus were found in the midthermocline region. Table 2 shows estimates of the addition of phosphorus to the epilimnion by the diffusion process.

Discussion

THE SETTLING BOTTLE TECHNIQUE

The settling velocity data show some gaps where values were not obtained due to equipment malfunction. The error bars shown are those calculated on the basis of one standard deviation for the difference between the concentrations in the top and bottom sections of the settling bottles, that is, the 68% confidence limits. This is considered adequate because a significant part of the variability between duplicates was not due to instrument or sampling inaccuracies but to the inhomogeneity of the suspension of particles (Sheldon et al. 1972). The size variation of the particles was large, ranging from approximately 1 μ to diatom chains of 5 mm in length. The effect of the sampling variability of particulates was reflected in the fact that it was not possible to obtain agreement between duplicate analyses, with particulates filtered from 1 to 2 liters of water, which was better than 5% of the measured value even when there had been a tenfold increase in concentration. Instrumental error is usually fairly constant and thus, the percentage disagreement between duplicates from this error tends to decrease as sample size increases. Because this relationship was not observed, it was concluded that most of the disagreement between duplicates resulted from the unequal distribution of particles, not instrumental error.

If the settling rate bottle is placed in surroundings having a different temperature from that of the contained water, vertical convection currents would be set up in the bottle. If these currents were strong enough to resuspend settled materials, erroneous results would be obtained. It is primarily for this reason that the settling is carried out in situ since the water in the bottle is at the same temperature as the surrounding water. However, this condition may not hold at depths close to the thermocline because the vertical movements of the thermocline would cause the temperature to vary at a specific depth. The results obtained in September, October, and March (Fig. 3) show thermocline settling velocities that are fairly consistent and lie between the values obtained in the upper and lower isothermal layers, indicating there was very little convective mixing in the bottles. If there had been such mixing, the settling velocities measured in the thermocline region would be close to zero; thus it is possible that the effects of temperature difference have been overestimated. A further advantage of the in situ experiment is that no changes are caused to orga-



LAKE ONTARIO STN. 19 JULY 19, 1972

LAKE ONTARIO STN. 19 SEPT. 7, 1972

LAKE ONTARIO STN. 19 OCT. 19, 1972

LAKE ONTARIO STN. 19 MARCH 7, 1973

FIG. 3. Settling velocity and temperature profiles, Stn. 19, Lake Ontario. (T.T. refers to the top of the thermocline.)

nisms whose settling velocities are sensitive to pressure differences, such as blue-green algae containing gas vacuoles.

A second complication is that the settling rate bottle may trap part of a zooplankton swarm or a large organic particle which is one of a widely dispersed population, such as a large zooplankton or a long algal chain. This would lead to a settling velocity value significantly different from those obtained at similar depths. This may be the cause for the high settling velocity obtained at 150 m in July 1972 (Fig. 3).

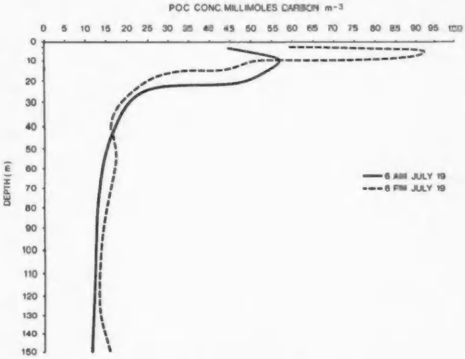


FIG. 4. Particulate organic carbon concentration profiles at Stn. 19, Lake Ontario, July 19, 1972.

Another source of error in calculating settling rates was leakage from the bottles on retrieval. This was immediately obvious because the total volume of samples drawn from the bottle was less than the bottle volume. The result of the leakage would be a low settling rate velocity since the water that leaked from the bottom of the bottle would contain much of the settled material.

The most obvious and perhaps most serious source of error is movement of the settling bottles on the mooring line during settling. Setting the subsurface float 10 m below the surface and having 225-kg weight of buoyancy prevented observable motion in the topmost bottles in any of the sea states when it was possible to place the mooring. It was not possible to set the mooring at wind speeds above 10 m sec^{-1} with the arrangements aboard the M. V. *Martin Karlsen.*

The currents in the Great Lakes are such that the mean flow in the surface waters of Lake Ontario is of the order of 10 cm sec^{-1} (F. M. Boyce, Canada Centre for Inland Waters, Burlington, Ont., personal communication) and the vane on the bottle has been seen to swing in a horizontal direction as it follows a change in current direction. The turbulence within the bottle associated with this type of motion would be small since the water inside

TABLE 1. Calculated additions of phosphorus to the epilimnion of Lake Ontario by the settling mechanism.

Date	Thermocline depth (*m*)	Settling velocity (*m* day^{-1})	Particulate phosphorus concn at thermocline depth (*mmoles P* m^{-3})	Settling flux (*mmoles P* m^{-2} day^{-1})	Settling flux addition to epilimnion (*%* day^{-1})
July 19, 1972	6	−0.32	0.23	−0.074	+2.2
Sept. 7, 1972	12	+1.68	0.20	0.336	−5.2
Oct. 18, 1972	52	+0.68	0.05	0.034	−0.14
Mar. 7, 1973	72	+0.61	0.07	0.043	−0.07

TABLE 2. Calculated additions of phosphorus to the epilimnion by the diffusion mechanism.

Date	Epilimnion quantity total phosphorus (*mmoles P* m^{-2})	Thermocline diffusion coef (m^2 day^{-1})	Thermocline gradient of total phosphorus (*mmoles P* m^{-4})	Diffusion flux (*mmoles P* m^{-2} day^{-1})	Diffusion flux addition to epilimnion (*%* day^{-1})
July 19, 1972	3.38	3.0	+0.046	−0.14	+4.1
Sept. 7, 1972	6.50	0.4	−0.040	+0.016	−0.2
Oct. 18, 1972	21.0	unknown	0.006	unknown	unknown
Mar. 7, 1973	53.4	unknown	0.0	0.0	0.0

moves with the bottle almost as a solid mass, as there are no air spaces. Eddies induced are horizontal and the likelihood of any settled material moving upward past the shutter plate is small. The effect of water mixing by bottle movement would cause the settling velocities to approach 0.0 m day^{-1} as the bottle depth decreased since the mixing effect would presumably be greatest near the surface. Since our results do not show surface settling velocities approaching zero, apparently the settled material was not being remixed into the water sample.

In general, values obtained on one cast in a particular depth zone generally fit with those from a different cast in the same zone, and also, the settling velocities in one zone change in a continuous fashion to those observed in another zone. These facts prove nothing in themselves but do indicate that realistic settling velocity values have been observed that are adequate for budget calculations.

The length of the top part of the settling bottle is 66 cm; thus if the water in the settling bottle is well mixed at the start of the experiment and the settling period is about 90 min, then the downward settling velocities of particles can be measured accurately only if they are less than 10.5 m day^{-1}. Similarly, the length of the bottom section of the bottle is 34 cm; thus only upward velocities of –7.0 m day^{-1} can be accurately measured. However, the maximum average velocity measured was 2.0 m day^{-1} (i.e. 20% of the maximum measureable velocity) and apparently the error introduced in the measurement of the average settling velocity by the limits of the method is acceptable.

Each of the four settling velocity profiles (Fig. 3) shows significantly different features but can be summarized into a general pattern which indicates that settling velocities increase slightly with depth to an intermediate zone of between 50 and 100 m; thereafter they decrease with depth. The settling velocities do not appear to be related to the thermal structure of the water column. A possible explanation is that the proportion of dead and senescent cells increases with depth and since dead cells (Reynolds 1973) and senescent cells (Smayda 1970) have higher settling velocities than living cells, the average settling velocity increases with depth. The question then arises as to why settling velocity decreases at the greater depths. A possible explanation is offered by Steele and Yentsch (1960) who found that older cells settled faster than rapidly growing cells but that the settling rate was considerably reduced when these cells were placed in the dark, in an enriched medium. By using a model in which the sinking rate decreased with depth, Steele and Yentsch (1960) were able to account for the chlorophyll profiles they had observed in the Atlantic Ocean. Possibly the decrease in observed settling velocities was due to fast-settling, senescent cells entering a dark, nutrient-rich zone in the lake and decreasing their settling velocities. Another possible explanation for lower settling velocities at greater depths is that particle size decreases with depth, but this has never been investigated in Lake Ontario and requires further examination since Sheldon et al. (1972) found in the ocean that particle concentration decreased with depth, but particle size did not.

SETTLING FLUXES

The settling fluxes shown in Table 1 can be considered only rough estimates of the actual fluxes on the days in question. The major cause of inaccuracy is that the experiments were conducted during daylight hours only, where a minimum 24-h measurement program is required. In addition opaque settling bottles were used which would have altered the response of phototactic organisms during daylight.

That phytoplankton can move up as well as down is well known. The upward movement of organic particulates is illustrated by Fig. 4 which shows changes in the concentration profile of particulate organic carbon.

In ecological models of ocean systems (Riley et al. 1949) and lakes (Vollenweider 1974; Wetzel et al. 1972), algal and detrital settling has been assumed et al. 1949) and lakes (Vollenweider 1974; Wetzel 1972), algal and detrital settling has been assumed as a mechanism for the removal of particulate organic carbon and associated nutrients from surface waters. However, the possibility must be considered that certain algal species absorb nutrients in the thermocline zone and subsequently move upwards to a zone of higher light intensity (Eppley et al. 1967). This would mean that negative algal settling could be a mechanism for the transport of nutrients upward from the thermocline to the surface waters, in a manner independent of water movements. Nutrients transported by negative settling can affect the epilimnion nutrient budget significantly and information on this process is essential for the development of sophisticated ecological models.

The most important result of the present investigation is that an estimate has been made of the net settling flux from the epilimnion and it has been demonstrated that negative settling can add appreciable quantities of nutrients to the epilimnion during the stratified period, as shown by the results of July 19, 1972 (Table 1). A second important consideration is that this result could not have been obtained by a sedimentation trap technique. If a sedimentation trap had been used, detrital material and downward settling algae would have been collected enabling the calculation of a downward settling flux. If this sedimentation flux was then used as an estimate of the net flux from the epilimnion, it would have led to serious error. Completely different epilimnion nutrient budgets would have resulted for the phosphorus addition to the epilimnion if a value of -1% per day had been used instead of +2% per day.

Another important result is that it is possible to compare the relative magnitudes of the settling flux and the diffusion flux; Table 2 shows that the two processes are of similar magnitude, occasionally acting in concert and occasionally in opposition. This means that a lake or ocean can have a variable response pattern. Should both the settling and diffusion processes add nutrients to the epilimnion a phytoplankton buildup could be expected; if the two processes are in opposition a steady-state condition in the epilimnion could result. Further, if the settling process was downward and significantly greater than the addition of nutrients to the epilimnion by diffusion, the surface waters would clarify.

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Microbiological Examination of Offshore Lake Erie Sediments

B. J. DUTKA, J. B. BELL, AND D. L. S. LIU

Department of the Environment, Environmental Management Service
Microbiological Laboratories
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

DUTKA, B. J., J. B. BELL, AND D. L. S. LIU. 1974. Microbiological examination of offshore Lake Erie sediments. J. Fish. Res. Board Can. 31: 299–308.

In August 1972 divers collected cores from the Central and Western basins of Lake Erie for microbiological analysis. The cores were sectioned and examined for sulfur cycle bacteria, nitrogen cycle bacteria, total heterotrophs, iron oxidizing bacteria, insoluble organic and inorganic phosphate solubilizing bacteria. Eh, nitrogen, organic carbon, and percentage moisture determinations were also made.

Data from these cores indicate that offshore sediments, not directly influenced by land inputs, contain similar, homogenously distributed bacterial populations which vary less than one order of magnitude between the sediment surface and the 5-cm level.

DUTKA, B. J., J. B. BELL, AND D. L. S. LIU. 1974. Microbiological examination of offshore Lake Erie sediments. J. Fish. Res. Board Can. 31: 299–308.

En août 1972, des plongeurs ont prélevé des carottes dans les bassins central et occidental du lac Erié en vue d'en faire l'analyse microbiologique. Nous avons sectionné les carottes et y avons cherché les bactéries du cycle du soufre, celles du cycle de l'azote, les hétérotrophes totaux, les bactéries oxydantes du fer et les bactéries capables de solubiliser le phosphate organique et inorganique insoluble. Nous avons également fait des déterminations d'Eh, d'azote, de carbone organique et d'humidité.

Les résultats obtenus avec ces carottes indiquent que les sédiments du large, non directement influencés par les apports terrestres, contiennent des populations bactériennes semblables, à distribution homogène, qui ne varient que par moins d'un ordre de grandeur entre la surface du sédiment et le niveau de 5 cm.

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ONE deficiency of lake and sediment microbiology is the lack of knowledge concerning bacterial physiological groups, their density and distribution patterns, and the role and origin of the transient and endemic populations in the sediments and overlying waters. It has been suggested that the microbial flora of sediments are the same irrespective of the sediments' source (Doetsch and Cook 1973). However, in studies of Lake Ontario and St. Lawrence River sediments, Vanderpost and Dutka (1971) found that some bacterial populations were closely correlated with local land usage. In addition, Dugan et al. (1970) found that agglutination and precipitation of microparticles, plus various adsorbed nutrients, by bacterially formed extracellular polymer fibrils play a role in sediment formation.

The present study represents the initial phase of a long-term program designed to investigate the distribution and density of various bacterial physiological groups in inshore and offshore sediments throughout the Canadian Great Lakes, and whether or not these populations are influenced by local inputs.

The Western and Central basins of Lake Erie were chosen as the initial study sites because they are probably representative of the most eutrophic offshore areas within Lake Erie and the Great Lakes. The sampling sites within these basins are widely separated, have similar sediment characteristics, and are not directly influenced by local inputs. The bacterial populations found in the sampling areas should, therefore, be truly indicative of endemic and/or acclimatized populations.

Materials and Methods

Sediment cores and overlying water samples were collected from the Western Basin (lat. N 41°45′42″, long. W 82°59′00″) at a depth of 10 m, and the Central Basin (lat. N 41°49′00″, long. W 82°12′00″) at a depth of 22 m (Fig. 1). Sediments in the sampling area are silty-clay mud deposits.

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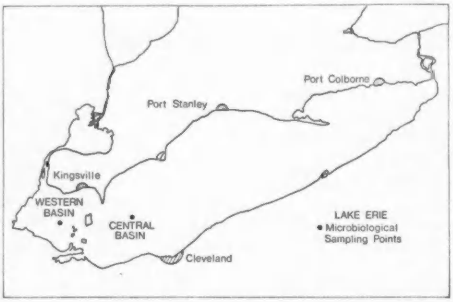

FIG. 1. Sediment and water sample collection sites in Lake Erie, August 28–29, 1972.

Divers, swimming against the current and using plastic tubes with sharpened edges collected six, 6.6 × 30–40 cm cores from each sampling site. All cores were collected within 1–2 m of each other and always upstream of previously collected cores.

Eh measurements (Kemp and Lewis 1968) were made on one core immediately after the divers had surfaced from the respective sites. The other cores were kept at 4 C until processing 18–20 h later.

In the laboratory, approximately 0.5 cm of the sediment circumference of each core was cut away with a sterile spatula to assure sediment integrity. The following sections of the five remaining cores from each site were pooled into sterile plastic bags and used as the reference samples: 0.0–0.5 cm; 0.5–1.0 cm; 1–2 cm; 3–4 cm; 5–6 cm; 10–11 cm; and 19–20 cm.

Immediately prior to sediment collection, sterile evacuated rubber bulbs held at arm's length ahead of a swimming diver were used to collect water samples 5 cm and 1 m above and immediately in front of the sediment collection area. The bulbs were sealed with sterile plugs, brought to the surface and held at 4 C until processing 18–20 h later. Water samples collected at the 1-m depth from the Central Basin were lost during transit from the sampling vessel to the laboratory.

LABORATORY PROCEDURES

Sample processing — From each sediment sample, the following subsamples were removed: (i) a 20-g sample for Most Probable Number (MPN) (APHA 1971) and plate count tests; (ii) a 10-g sample that was dried at 41.5 C to stability, to establish a wet:dry ratio; (iii) a 10-g sample for respiration studies; (iv) a 5–10-g sample for nitrogen and organic carbon analysis.

MPN and plate count tests — Ten grams sediment and 100 ml phosphate buffer (APHA 1971) were blended for 1 min at moderate speed. Immediately after blending, aliquots were removed and tested for the following bacterial physiological groups: ammonifying, nitrifying, denitrifying, nitrate reducing, organic sulfur reducing, sulfur oxidizing, sulfate reducing, iron oxidizing, manganese oxidizing, inorganic and organic phosphate solubilizing bacteria. The blended sample was also used for estimating heterotrophic populations using a low nutrient medium and a spread plate technique (Bell and Dutka 1972).

Ammonifying bacterial densities were estimated in casein solution (Allen 1953), nitrifying bacterial densities in Nitrosomonas Broth (Thompson 1969). Alexander's (1965) medium was used to test for denitrifying bacteria (N_2 production) and nitrate reducing bacteria (NH_3 and NO_2 production). All nitrogen cycle bacterial tests were incubated for 21 days at 28 C.

Density estimates of the sulfur oxidizing bacterial population were made in Postgate's *Thiobacillus* medium (Postgate 1966) with incubation at 28 C for 14–21 days. Sulfate reducing bacteria were enumerated in Starkey's medium (Starkey 1948) with an anaerobic incubation period of 14–21 days at 28 C. For the enumeration of bacteria that reduce organic sulfur to sulfides, an MPN medium described by Gunkel and Oppenheimer (1963) was used, combined with anaerobic incubation at 28 C for 14–21 days.

Density of iron oxidizing bacteria was estimated in Winogradsky medium (Rodina 1972) using MPN techniques with a 7–10-day incubation at 20 C. Density of manganese oxidizing bacteria was estimated using manganous sulfate and manganous acetate salts in a medium developed by Timonin et al. (1972) with incubation at 28 C for 7–14 days.

Populations of inorganic phosphate solubilizing bacteria were estimated using the special hydroxyapatite medium of Ayyakkannu and Chandramohan (1971) with incubation at 28 C for 14 days. Tests for insoluble organic phosphate solubilizing bacteria were carried out on Odoevskaia's (1961) potato agar with incubation at 28 C for 14 days.

Respiration studies and chemical analysis — Organic carbon estimates were obtained by combustion of dried samples as described by Kemp and Lewis (1968). Total nitrogen was determined by a method described by Keeney and Bremner (1967).

Oxygen consumption by the various sediment sections was measured at 20 and 4 C using a Gilson Differential Respirometer. Each Warburg flask contained 3–5 g of sediment (wet weight), 1 ml of 0.2 μ membrane filter-sterilized lake water and in the center well, 0.2 ml of 20% KOH for CO_2 absorption. A preincubation period of 10 min was used.

Similar oxygen consumption studies using Western Basin core sections treated with 0.5 ml of 0.1 M KCN and Na Azide were performed in an attempt to ascertain whether chemical or biological processes at the sediment surface and throughout the core created the greater oxygen demand.

Results and Discussion

Because of the distance between the sampling site and the laboratory, it was not possible to collect the samples and perform all analyses within our usual time frame of 2–3 h. However, as the sampled core temperatures varied from 10 C at the surface to 6 C at 25 cm, it is highly unlikely that significant changes occurred in the bacterial populations between collection and testing.

In testing for bacterial populations, temperatures varying from 20 to 28 C were chosen to facilitate enumeration procedures. It is recognized that in so doing, there is a possibility of selection occurring. However, in comparison studies we have found that enumeration samples incubated at 4 and 20 C yield similar total populations, when the 4 C incubation period was extended. Studies of Lake Ontario sediments by Bell and Dutka (1972) indicate that these sediments do not contain any true psychrophiles. From Doetsch and Cook's (1973) review of bacterial temperatures the majority of organisms found in Great Lakes sediments are probably facultative psychrophiles and thus 20 and 28 C should be satisfactory for bacterial density studies.

Oxidation-reduction potentials have frequently been used to delineate aerobic and anaerobic sediments. Recent studies by Hargrave (1972a) indicate that no oxygen is present in sediments with Eh values below +100 mv. Eh values presented in Fig. 2 indicate the cores are apparently devoid of oxygen and have similarly reduced Eh profiles, in spite of the rather large differences in organic content between Central and Western Basin cores.

Data presented in Table 1 indicate a surprisingly large difference in oxygen uptake rates between Central and Western Basin sediments. As lake sediments with the lowest Eh potentials (highest reducing intensity) have the highest oxygen consumption (Hargrave 1968), the similarity between the cores' Eh profile and bacterial populations indicate other factors must be involved to account for the difference in core oxygen uptake rates. Ryback's (1969) studies have shown that different rates of oxygen uptake by various sediments could be explained by differences in organic matter present for oxidation. Therefore, one factor that must be considered in trying to explain the difference in oxygen uptake rates between the core areas is the nature and amount of organic material present in these sediments.

The shallower Western Basin sediments are frequently disturbed by wind–wave action, causing resuspension of organic materials that are further degraded by bacterial action. Thus the degree of degradation of the sedimented organic material in the Western Basin is much greater than that in the Central Basin. This is shown in Fig. 2 by the greater concentration of organic material in Central Basin sediments.

To answer the question whether chemical or biological oxygen demand predominates in these sediments, one set of sediment samples was inactivated by poisoning with sodium azide and potassium cyanide. Table 2 shows that in the surface sediment 0–1-cm level, approximately 75% of the oxygen demand is biological whereas in the lower sediments the biological oxygen demand varies from 11 to 45%.

The majority of oxygen demand studies were performed at 20 C. Because this temperature gives potential rather than actual oxygen uptake, an attempt was made to ascertain oxygen demands at 4 C, a temperature more commonly found in Great Lakes sediments. Data presented in Table 1 indicate that uptake rates varied from 45% of those found at 20 C at the sediment surface to 73% at the 10-cm depth. These findings reflect decreased bacterial activity normally related to lowered temperature and the maintenance of the less temperature-sensitive chemical oxygen demand in the sediments.

Heterotrophic bacterial populations found in this study (Fig. 3) illustrate the typical distribution patterns encountered in the lower Great Lakes sediments (Bell and Dutka 1972; Vanderpost 1972). Surface sediment heterotrophic bacterial densities in these lakes consistently range between 10^6 and 10^7 organisms per gram dry weight, no matter what counting medium has been used, or what year or month the sample has been collected (Weeks 1944; Vanderpost 1972 and Bell and Dutka 1972).

Heterotrophic bacteria are found wherever sufficient organic matter is present, in concentrations that are usually proportional to the amount of organic matter available. Although more than optimal amounts of organic nutrients are present in these sediments, the heterotrophic bacterial populations are a reflection of the number of heterotrophs capable of surviving by a facultative mechanism in a deoxygenated environment. This assumption is well supported by Jones' (1971) study which showed that heterotrophic populations in sediments are positively correlated to the dissolved oxygen tension.

Sulfur cycle bacterial data (Fig. 3) illustrate the close similarity between Lake Erie Central and Western Basin sediments and the homogeneity of the top 4–6 cm of these sediments. Sulfate reducing bacteria were found to maintain their population levels throughout the core, with approximately one order of magnitude difference between the surface (10^5) and the 20-cm level (10^4). This population maintenance is probably related to the rather constant negative Eh values and the availability of carbonaceous energy sources, probably algae.

The large organic sulfur reducing populations are indicative of a ready supply of organic material (algae) and are potential producers of a ready energy for the sulfate reducing bacteria. The increase in density of the sulfur oxidizing bacteria in the top 3 cm of obviously reduced sediments indicates the existence of microecosystems where conditions are favorable for their growth. In the deeper sediments, where a decrease in sulfur oxidizing populations is expected, we are probably measuring the existence of a dormant population. Core distribution of sulfate reducing and sulfur oxidizing bacterial populations in this study were very similar to those found by Vanderpost (1972) in the silty-clay sediments of Lake Ontario.

Figure 4 presents nitrogen cycle bacterial data. Densities at or near the sediment–water interface are very similar from one basin to the other. Deeper

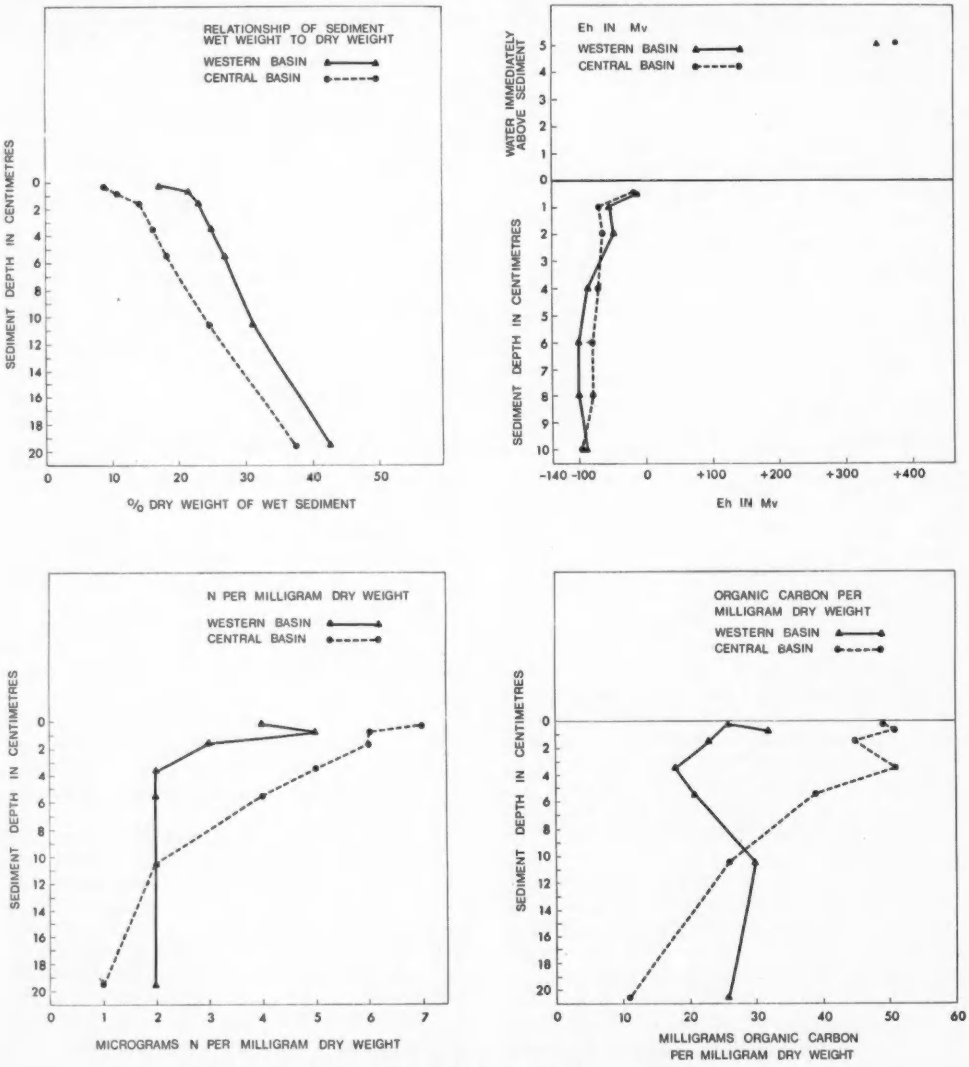

FIG. 2. Physical and chemical data obtained from collected cores.

sediment data indicate some divergence of counts, especially with the ammonifying and denitrifying populations which were found to vary approximately one–two orders of magnitude from one basin to the other.

The large ammonifying populations in these sediments are probably a good indication of the availability of a ready source of complex nitrogenous substances. It is believed that the ammonia produced by these bacteria stimulates the growth of autotrophic bacteria that obtain energy by oxidizing ammonia through nitrite to nitrate. Because of the oxygen used in this process, plus that utilized by the large heterotrophic bacterial population, drastic reductions in oxygen levels can occur. Support for the concept of bacterial depletion of oxygen in Lake Erie has been provided by Burns and Ross (1972) who found that bacterial oxidation of organic materials (algae) was responsible for 88% of the oxygen depletion and occurred mainly at the sediment–water interface.

TABLE 1. Oxygen uptake rates of the sampled sediments.

Station	Sediment depth (*cm*)	μliter O_2/h/g sediment dry wt 20 C	μliter O_2/h/g sediment dry wt 4 C
Western Basin Lake Erie 41°45′42″N 82°59′00″W	0.0–0.5	201	91
	0.5–1.0	194	100
	1–2	205	130
	3–4	203	131
	5–6	203	133
	10–11	174	127
	19–20	182	101
Central Basin Lake Erie 41°49′00″N 82°12′00″W	0.0–0.5	382	
	0.5–1.0	516	
	1–2	416	
	3–4	416	
	5–6	232	
	10–11	108	
	19–20	128	

An anomaly in the nitrogen cycle data is the rather consistent maintenance of the nitrifying bacterial populations throughout the core depth, especially as oxygen is an obligate requirement for *Nitrosomonas* and *Nitrosococcus* species that are believed to be involved in this process. Since sampling and core-cutting procedures have ensured the integrity of the core and the culture medium is specific for autotrophic nitrifying bacteria, the presence of autotrophic nitrifying bacteria throughout the cores indicates that either microzones are present or we are measuring dormant populations.

Studies by Ayyakkannu and Chandramohan (1970, 1971) indicate that the major portion of potentially available phosphate is locked up as insoluble organic and inorganic phosphorus compounds in sediments and soils. They also noted a relationship between phosphate content, the numbers of phosphatase solubilizing bacteria, and phosphatase activity in sediments.

Since bacterial phosphatase activity may regulate the phosphate content of sediments, and in turn, especially under anaerobic conditions, may influence the phosphate level of overlying waters, it was decided to test for phosphate solubilizing bacterial populations on an exploratory basis.

Data presented in Fig. 5 indicate that these sediments contain a fairly large bacterial population with phosphatase activity, especially in the top

TABLE 2. Relationship between biological and chemical oxygen uptake rates.

Station	Sediment depth (*cm*)	μliter O_2/h/g sediment dry wt 20 C	μliter O_2/h/g sediment dry wt 20 C (KCN and azide)	% Inhibition by KCN and azide
Western Basin Lake Erie 41°45′42″N 82°59′00″W	0.0–0.5	201	74	63
	0.5–1.0	194	23	88
	1–2	205	182	11
	3–4	203	167	18
	5–6	203	155	24
	10–11	174	135	22
	19–20	182	99	45

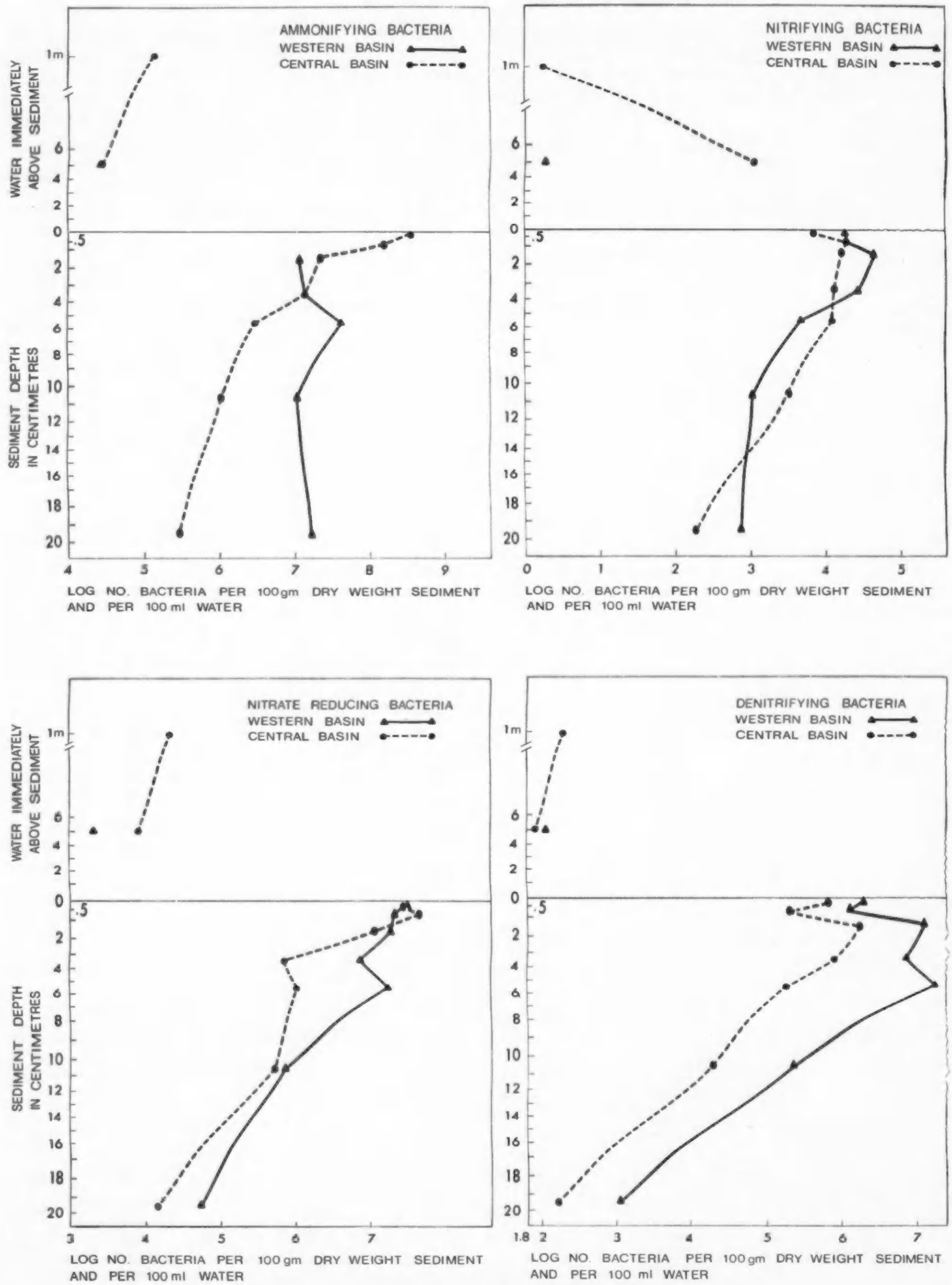

FIG. 3. Distribution of heterotrophic bacteria and sulfur cycle bacteria.

5–6 cm, with the Western Basin sediments having the greater population. With the exception of Western Basin bacterial populations capable of solubilizing insoluble organic phosphate, all other phosphatase producing bacterial populations tended to show a marked decrease at the 10-cm level. Because of the unreliability of sediment phosphate estimating techniques, no determinations of phosphate concentration were performed on these sediments. Therefore, it is not known whether this

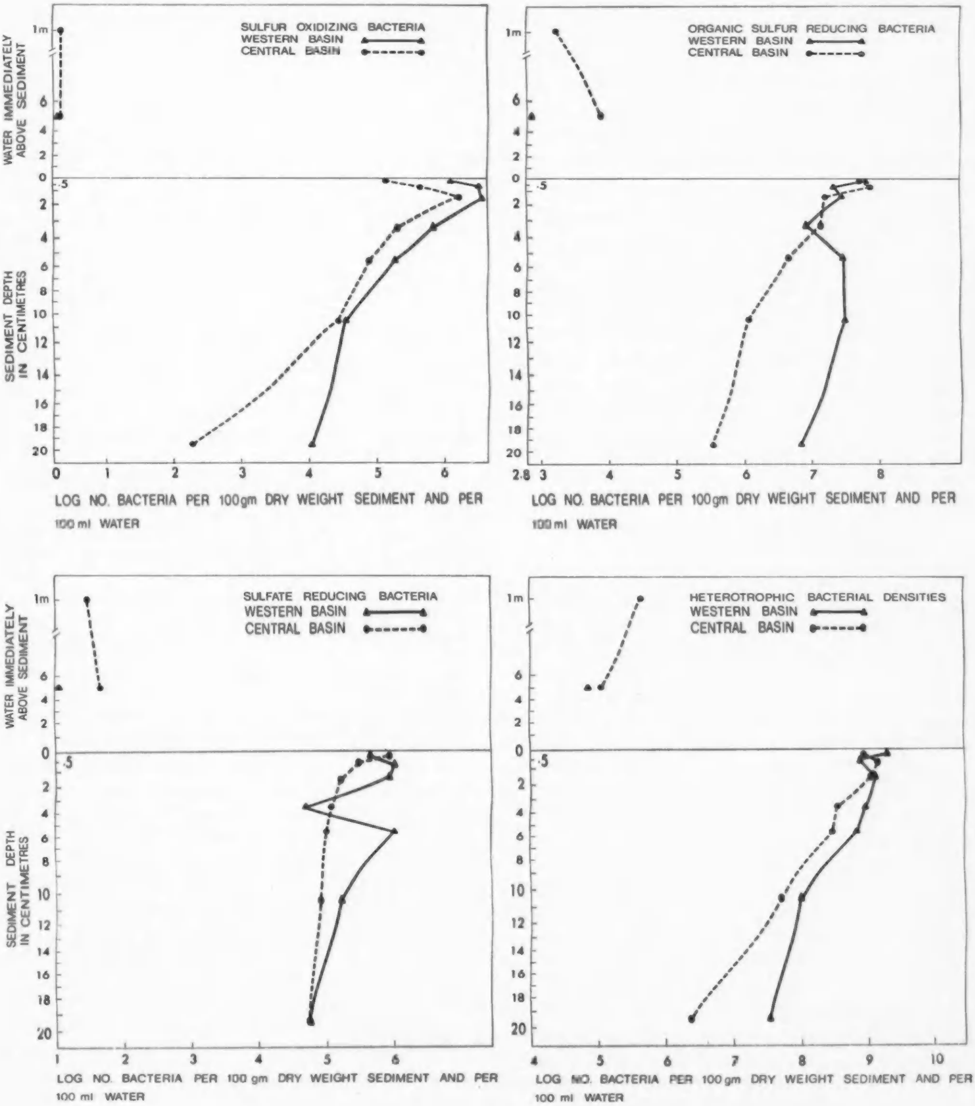

FIG. 4. Distribution of bacteria involved in various phases of the nitrogen cycle.

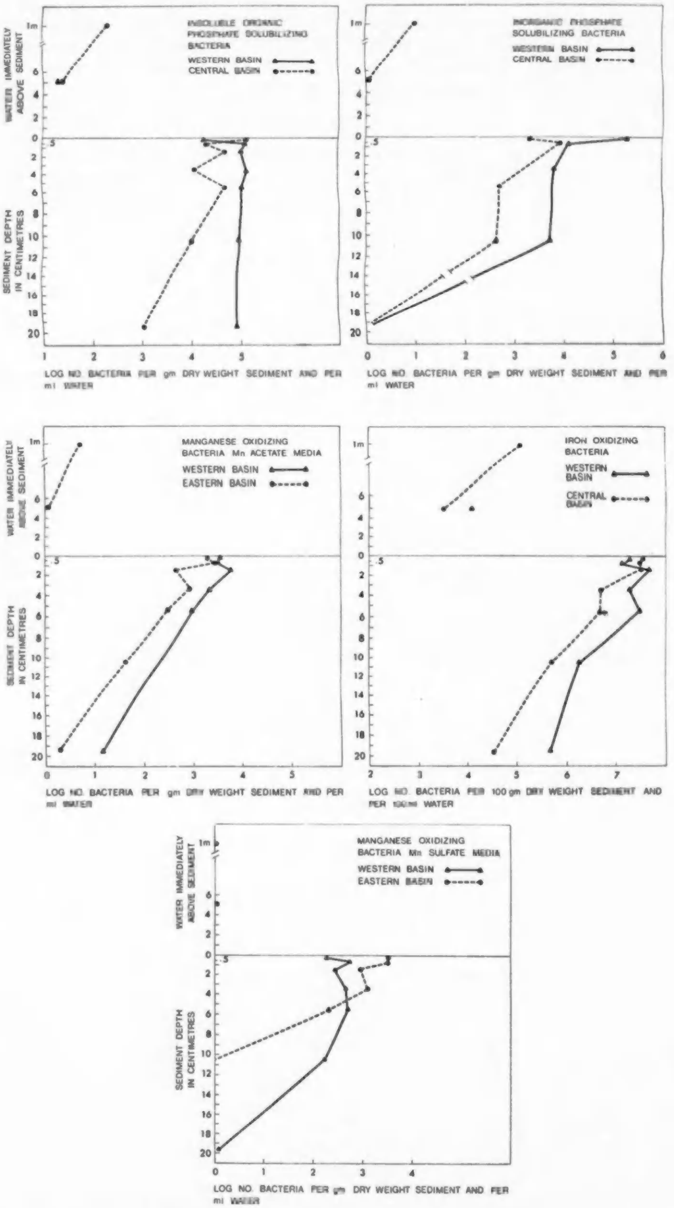

FIG. 5. Distribution of phosphate solubilizing, iron, and manganese oxidizing bacteria in the sediments and overlying waters.

population decrease was due to conditions inhibitory to phosphatase production and activity or to the lack of certain specific insoluble phosphates.

Aquatic bacteria play a major role in the oxidation and precipitation of manganous and ferrous ions, and in the reduction of their oxidized forms to soluble forms. Ehrlich (1962) has shown that nodule formation is much faster in the presence of oxidizing bacteria than in their absence. Therefore, sediment samples were collected to investigate the relationship between iron and manganese oxidizing bacterial populations and ferro-manganese oxide nodules. No nodules were present at the sampled sites, although bacterial populations varying from 10^5–10^7 per 100 g of sediment and capable of oxidizing iron and manganese were found (Fig. 5).

Two media, each containing a different manganous salt (sulfate and acetate) were used in this study to ascertain whether or not bacteria capable of oxidizing manganese had a specific salt preference. There was no significant difference in the top 3–4 cm of sediment between Central and Western Basin manganese oxidizing populations. Bacterial populations capable of utilizing manganous sulfate were very low in the deeper sediments, disappearing completely in the Western Basin at the 10-cm level.

Iron oxidizing populations exhibited the typical distribution pattern noted for most bacteria in these sediments, i.e. no apparent difference in bacterial densities between Central and Western Basin sediments. A homogenous distribution of iron oxidizing bacteria was found within the top 5 cm and a break in the population at the 6-cm level with a gradual two-order of magnitude decrease in population to the 20-cm level.

Throughout this study bacterial populations in the overlying waters were usually two or more orders of magnitude less than those encountered in the surface sediments, as would be expected of a surface area-influenced population. Contrary to data presented by Menon et al. (1972) and Taylor (1940) a slight decrease in population was noted from the 1-m level to the 5-cm level with the notable exception of nitrifying bacterial populations, that increased by three orders of magnitude from the 1-m to the 5-cm level. This increased population may be related to the high ammonifying population creating a ready nutrient source.

Hargrave (1972b) has shown that a relationship exists between the surface area and organic content of sediments, and the density and metabolism of endemic bacteria. Bacteria in sediments are primarily epipsammic. The Lake Erie silty-clay mud sediments provide amounts of surface area that support bacterial populations in relation to the available oxygen tensions, temperature, and nutrient supply, which in Lake Erie is largely sedimented algae (Anthony and Hayes 1964). However, once a balanced bacterial population is reached it is suspected that the addition of organic nutrients and detritus to this system does not necessarily stimulate the production of a greater bacterial biomass. Confirmation of this belief was given during Project Hypo (Burns and Ross 1972) where it was shown that detrital sedimentation in Lake Erie can be in the form of massive algal 'rains' that, although providing added nutrients, also tend to bury the endemic population. Thus, even though additional nutrients are available, only the surface populations, many of which have been brought down by the algae, are actively involved in their destruction. This results in a slow build-up of undecomposed material with a potential oxygen demand and a fairly stable bacterial population.

From these and previous microbiological studies of the lower Great Lakes sediments, microbiological data indicate that there is a fairly stable, homogenously distributed population which varies less than one order of magnitude between the surface and the 5-cm depth. Furthermore, the presented and referenced data support the belief that within these lower Great Lakes similar bacterial populations are present in sediments not directly influenced by land usage.

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Seasonal Abundance of Crustacean Zooplankton and Net Plankton Biomass of Lakes Huron, Erie, and Ontario

N. H. F. WATSON AND G. F. CARPENTER[1]

Department of the Environment, Fisheries and Marine Service
Great Lakes Biolimnology Laboratory
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

WATSON, N. H. F., AND G. F. CARPENTER. 1974. Seasonal abundance of crustacean zooplankton and net plankton biomass of lakes Huron, Erie, and Ontario. J. Fish. Res. Board Can. 31: 309–317.

Crustacean zooplankton concentrations (numbers per m^3) in the upper 50 m found in lakewide cruises during all or most of the seasons on lakes Ontario and Erie in 1970 and on Lake Huron in 1971 showed that the species of zooplankton crustaceans present in the three lakes were generally identical, although the times of maxima and relative species compositions differed. Calanoid copepods were most abundant and diverse in Lake Huron and western Lake Erie. Cyclopoids and cladocerans were most abundant in lakes Erie and Ontario and in the Saginaw Bay region of Lake Huron. The most abundant cyclopoid throughout the year in all three lakes was *Diacyclops bicuspidatus thomasi*; *Tropocyclops prasinus* and *Acanthocyclops vernalis* were abundant especially in lakes Ontario and Erie, respectively. Cladocerans were most numerous in lakes Erie and Ontario. Numbers of individuals fluctuated markedly through the season with maxima in the spring or summer months in all three lakes.

Biomass values (ash-free dry weight) were highest in Lake Erie, especially the Western Basin, and in Saginaw Bay of Lake Huron. Although numbers of crustaceans/m^3 were much lower in Lake Huron than in Lake Ontario, net biomass values were similar. This was due to the greater size and average weight of crustaceans in Lake Huron samples. Inshore waters of lakes Ontario and Huron and all three basins of Lake Erie were subject to greater fluctuations in concentrations of crustacean zooplankton and net biomass values than in the pelagic waters of lakes Ontario and Huron.

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Les concentrations de crustacés planctoniques (nombre par m^3) observées dans les 50 m supérieurs au cours de croisières effectuées à la grandeur du lac, à toutes ou presque toutes les saisons, sur les lacs Ontario et Erié en 1970 et sur le lac Huron en 1971 démontrent que les espèces de crustacés planctoniques sont en général identiques dans les trois lacs, bien que les périodes de maxima et la composition relative en espèces soient différentes. Les copépodes calanoïdes sont plus abondants et plus diversifiés dans le lac Huron et dans le lac Erié occidental. Les cyclopoïdes et les cladocères sont plus abondants dans les lacs Erié et Ontario, et dans la région de la baie Saginaw du lac Huron. *Diacyclops bicuspidatus thomasi* est le cyclopoïde le plus abondant, durant toute l'année, dans les trois lacs, alors que *Tropocyclops prasinus* et *Acanthocyclops vernalis* sont particulièrement abondants dans les lacs Ontario et Erié respectivement. Les cladocères sont le plus nombreux dans les lacs Erié et Ontario. Le nombre d'individus accuse des fluctuations saisonnières marquées, avec maxima au printemps ou en été dans les trois lacs.

La biomasse (poids sec sans les cendres) a une valeur maximale dans le lac Erié, surtout dans le bassin occidental, et dans la baie Saginaw du lac Huron. Bien que le nombre de crustacés/m^3 soit beaucoup moindre dans le lac Huron que dans le lac Ontario, la biomasse du plancton tamisé est la même dans les deux lacs. Ceci est dû au fait que, dans les échantillons du lac Huron, les crustacés ont une taille et un poids moyen plus grands. Les eaux du littoral des lacs Ontario et Huron et des trois bassins du lac Erié subissent de plus grandes variations de concentration des crustacés planctoniques et de biomasse du plancton tamisé que les eaux du large des lacs Ontario et Huron.

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[1] Present address: Industrial Biotest Laboratories Inc., Northbrook, Ill. 60062, USA

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MOST studies on the communities of crustacean zooplankton of the Great Lakes, with the exception of Patalas (1972), have been limited to one of the lakes or to a specific group of animals (i.e. Davis 1966, 1969; Patalas 1969; Robertson 1966; Gannon and Beeton 1971). These studies have also been limited to short periods of time and do not provide information on the seasonal changes in abundance of the plankton.

This report gives the general aspects of abundance and species composition of crustacean zooplankton of lakes Ontario, Erie, and Huron during all or most of the seasons in 1 yr. Vertical net hauls were taken at 33 stations on 13 cruises on Lake Ontario from January to December in 1970, at 30 stations on 10 cruises on Lake Erie from April to December in 1970, and at 14 stations on 8 cruises on Lake Huron from May to November in 1971. More detailed descriptions of the distribution and abundance of the crustacean zooplankton of the lakes are being prepared as a series of technical reports, (Nauwerck et al. 1974; and Watson et al. 1974).

Materials and Methods

Samples were obtained from single hauls with a net of 64 μ nylon mesh, 0.4 m in diameter, from a depth of 50 m or from 2 m from bottom in shallower locations. In Lake Ontario 17 stations representing about 20% of the surface area were at depths of less than 50 m and were designated as littoral (Munawar and Nauwerck 1971), the remainder being in the pelagic zone. In Lake Erie, five stations were in the shallow Western Basin, representing 15% of the surface area of the lake; 20 were in the Central Basin, representing 15% of the surface area; and the remaining eight were in the Eastern Basin, representing the remaining 20% of the surface area. Cruise means estimates of crustacean concentration for these two lakes are weighted on a surface area basis. For Lake Huron, data from 11 stations on a transect from the Straits of Macinac to a point off the origin of the St. Clair River were used to produce the main lake values of zooplankton abundance for Lake Huron and data from two stations for Saginaw Bay. Particulate carbon values were from 31 stations over the lake and two from Saginaw Bay. For station patterns on lakes Ontario and Huron see Carpenter et al. 1974 (this issue) and for Lake Erie, Glooschenko et al. (this issue).

The sample from each station on each cruise was divided into three equal volumes for analyses.

One portion was preserved in 4% formalin for specific identification of the crustaceans and estimates of the abundance of animals in the water column. Examinations were made through an inverted compound microscope. Two or more 1-ml subsamples of the well-mixed sample were taken with a wide-bore pipette and at least 200 animals exclusive of copepod nauplii were identified and enumerated. Numbers/m^3 for each station were calculated from percent of sample counted, assuming 100% straining of the water column, depth of tow and net diameter. The other portions of the sample were collected on prewashed, preweighted GF/C glass fibre filters. One was dried in a desiccator at room temperature, weighed, heated in a muffle furnace at 600 C for 30 min, and reweighed to determine the weight of organic material retained in the 64-μ net. Ash-free dry weight was used as a measure of organic seston to eliminate the effects of various amounts of inorganic sediment present at different points in the lakes. The third portion was extracted in acetone by the method of Glooschenko et al. (1972) to determine the amount of chlorophyll in the net sample.

Estimates of crustacean biomass were made by multiplying cruise mean values for each species by average weights, determined for most species by B. Wilson, Department of Zoology, University of Guelph, (unpublished data) from animals collected from Lake Ontario on cruises conducted during the International Field Year for the Great Lakes.

Results

The highest concentrations of crustacean zooplankton and particulate organic matter in net hauls from the upper 50 m were found in Lake Erie (Fig. 1). Similar high concentrations of crustaceans (max 324,000/m^3) were found in the Saginaw Bay region of Lake Huron. Marked seasonal changes in standing crops of zooplankton were accompanied by less pronounced changes in organic material in the net hauls. There was no simple relationship between crustacean zooplankton concentration and weight of organic material. Apparently seasonal changes in the species composition and number of individuals as well as the amount of net phytoplankton are responsible in large part for the discrepancies.

With few exceptions, we found the same species of crustacean zooplankton in samples from all three lakes (Table 1–3).

Lake Huron and to a lesser extent the Western Basin of Lake Erie had the largest numbers and the most species of calanoid copepods, about 30–60% of the crustacean concentrations in Lake Huron, 15% in Western Lake Erie, and 5–10% in Lake Ontario. We did not find *Diaptomus ashlandi* in Lake Ontario as reported by McNaught and Buzzard (1974) nor did we find *D. pallidus* at any open lake stations in lakes Erie and Ontario as reported by Patalas (1972).

Limnocalanus macrurus was found in all lakes although we were probably not sampling deeply enough to sample its abundance quantitatively. In Lake Erie we found both adults and juveniles of this species at several stations although numbers were low. This indicates a low but widespread resident population in the lake in 1970. *Eurytemora affinis*, believed to be a recent marine invader, was found in low concentrations in lakes Ontario, Erie, and Huron at many inshore stations, especially in late summer. Concentrations of *Epischura lacustris* were low in all lakes.

Diacyclops bicuspidatus thomasi was the most abundant cyclopoid in many samples, especially in lakes Ontario and Erie. At some stations in the Central and Eastern basins of Lake Erie, concentrations of this species exceeded 200,000/m^3, mostly juveniles in June and July 1970. *Acanthocyclops vernalis* was numerous only in the Western Basin of Lake Erie. *Tropocyclops prasinus* was present in all the lakes in low numbers but was most frequently found in Lake Ontario. *Mesocyclops edax* was common in summer, especially in Lake Erie.

Cladocerans were most numerous in Lake Erie, especially in the Western and Central basins. We found *Bosmina longirostris* and *Eubosmina coregoni* most frequently, and a form possibly attributable to *E. longispina* on a few occasions. In lakes Ontario and Erie *B. longirostris* was generally found earlier in the summer followed by *E. coregoni* and *E. longispina*. The most commonly found *Daphnia* species in the three lakes were *D. retrocurva*, *D. galeata mendotae*, and *D. longiremis*. No specimens clearly identifiable as *D. pulex* were found in Lake Erie. *Ceriodaphnia lacustris* was numerous in summer in the open waters of the lakes and *Chydorus sphaericus* was sporadically abundant especially in western Lake Erie. Of the larger cladocerans, *Leptodora kindtii* was present in quantities especially in lakes Erie and Ontario; *Holopedium gibberum* and *Polyphemus pediculus* were most abundant in the upper lakes.

In general, abundance and variety of cladocerans were extremely low in early spring, increased rapidly in the summer, and declined in the fall. In the Western Basin of Lake Erie and Saginaw Bay of Lake Huron these forms were the most abundant crustacean zooplankton, with a series of species succeeding each other throughout the sampling period.

Estimated zooplankton biomass was compared with the total net biomass and plankton net chlorophyll (Table 4). Though units of the three biomass measures are not strictly comparable, changes in net phytoplankton as measured by chlorophyll concentration appears to account for most of the difference between ash-free net biomass and estimated crustacean biomass.

Cruise mean values for net chlorophyll varied from less than 0.5 mg/m^3 in Lake Huron to a maximum of close to 2 mg/m^3 in lakes Erie and Ontario. The relation of net to total chlorophyll (expressed as a percent) was highest in the spring

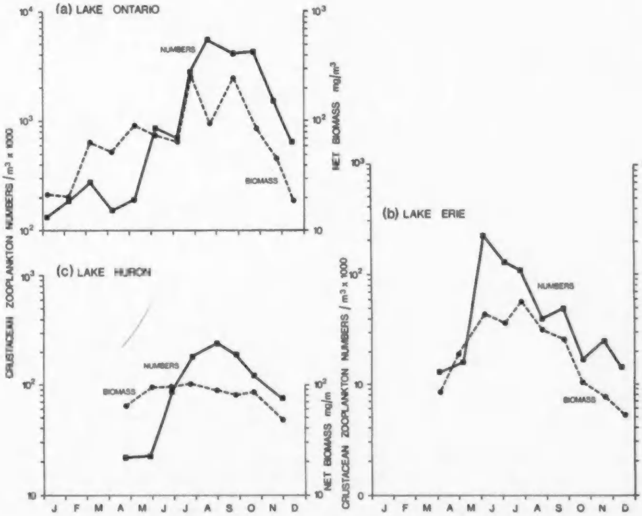

FIG. 1. Mean number of crustaceans/m^3 and plankton net biomass on each cruise for Lake Ontario 1970, Lake Erie 1970, and Lake Huron 1971. Values for lakes Ontario and Erie are weighted on a surface-area basis.

TABLE 1. Mean concentrations (numbers/m³) of crustacean zooplankton (33 stations, one haul from upper 50 m at each) for 13 cruises on Lake Ontario in 1970.

Species	6–11 I	3–8 II	3–8 III	31 III–4 IV	28 IV–1V	25–29 V	22–27 II	16–20 VII	17–21 VIII	14–19 IX	13–17 X	16–20 XI	7–11 XII
Bosmina longirostris	6	52	152	61	86	430	1137	18933	19210	5150	13700	2098	173
Eubosmina coregoni	9	1	5	0.4	4	420	13	12	306	1753	2254	145	35
Daphnia spp.	–	–	4	–	3	3	7	161	6868	5295	3296	352	57
Ceriodaphnia lacustris	–	–	–	–	–	–	–	69	448	712	1146	2	–
Chydorus sphaericus	–	–	–	–	1	27	1	31	176	520	984	36	6
Leptodora kindtii	–	–	–	–	–	–	–	3.3	98	58	8.4	–	–
Holopedium gibberum	–	–	–	–	–	–	–	–	–	22	–	–	–
Alona affinis	–	–	–	–	–	–	–	–	–	14	2	2	–
Diacyclops bicuspidatus thomasi –adults	166	170	415	424	727	241	1123	1532	3371	3545	1829	482	246
Acanthocyclops vernalis –adults	–	–	–	–	–	–	–	73	616	197	19	7	6
Tropocyclops prasinus mexicanus –adults	78	75	71	33	57	23	9	26	548	1692	3827	1824	527
Mesocyclops edax–adults	–	–	–	–	–	–	–	–	207	59	31	–	–
Cyclopoid juveniles	758	1399	1685	566	445	3104	4499	6274	21316	15018	14391	9933	5028
Limnocalanus macrurus –adults and juveniles	137	225	131	179	440	227	227	42	185	167	57	52	28
Diaptomus sicilis and *D. oregonensis* –adults	30	49	48	23	18	11	22	50	60	82	53	77	–
Diaptomus minutus–adults	59	57	111	98	49	26	19	120	204	52	9	60	–
Diaptomus juveniles	83	73	224	65	58	146	222	267	725	634	685	475	208
Eurytemora affinis –adults and juveniles	–	–	–	4	–	0.9	–	14	401	129	68	10	1

TABLE 2. Mean concentrations (numbers/m³) of crustacean zooplankton (30 stations, one haul from upper 50 m at each) for 10 cruises on Lake Erie in 1970.

Species	7–11 IV	6–10 V	2–6 VI	3–7 VII	28 VII–1 VIII	25–29 VIII	23–27 IX	21–25 X	25–30 XI	14–18 XII
Bosmina longirostris	1330	978	34523	4974	165	215	595	1617	6786	4460
Eubosmina coregoni	217	102	41596	10522	16289	2831	7315	3247	1440	734
Daphnia spp.	73	120	10248	39426	29068	12873	4953	1547	1696	345
Ceriodaphnia lacustris	–	–	–	–	123	198	65	19	14	–
Diaphanosoma leuchtenbergianum	–	2	–	14	46	1467	394	134	40	4
Holopedium gibberum	–	–	7	–	–	72	44	21	13	0.6
Leptodora kindtii	3	–	8	401	40	91	31	5	–	–
Chydorus sphaericus	142	190	546	429	1068	6152	16815	2239	2125	375
Alona affinis	–	–	–	40	–	–	17	3	–	0.9
Eurycercus lamellatus	–	–	–	–	–	–	6	13	3	–
Latona setifera	–	–	–	–	–	–	–	0.7	–	–
Leydigia acanthocercoides	–	–	–	–	–	–	–	–	4	1
Diacyclops bicuspidatus thomasi –adults	3827	4067	10429	5153	4826	823	457	766	1403	762
Diacyclops bicuspidatus thomasi juveniles	5217	9626	99634	71768	36412	4758	1966	3030	7759	6402
Acanthocyclops vernalis Fischer adults	5	21	121	929	121	46	205	53	173	50
Acanthocyclops vernalis Fischer juveniles	21	99	1077	2274	1103	170	876	586	765	332
Tropocyclops prasinus mexicanus –adults	28	2	–	–	57	63	62	24	36	46
Tropocyclops prasinus mexicanus juveniles	6	4	14	11	10	13	14	7	12	28
Mesocyclops edax –adults	1	29	970	988	4871	1146	935	466	6	3
Mesocyclops edax –juveniles	6	68	96	756	4288	2759	3445	1805	248	59
Eucyclops agilis –adults and juveniles	–	–	–	–	–	–	–	0.7	–	–
Eucyclops speratus –adults and juveniles	–	–	–	–	–	–	–	–	4	–
Limnocalanus macrurus –adults	6	8	7	9	–	–	6	–	–	8
Limnocalanus macrurus –juveniles	–	23	–	21	–	14	–	4	–	–
Diaptomus sicilis–adults	8	20	370	302	1066	206	169	56	20	16
Diaptomus oregonensis –adults	554	77	182	1673	4610	2075	2202	718	1233	566
Diaptomus minutus –adults	637	199	848	444	1217	214	117	31	–	36
Diaptomus siciloides –adults	48	13	79	135	167	174	214	5	5	16
Diaptomus ashlandi –adults	139	21	899	99	44	–	20	5	1	66
Diaptomus –juveniles	204	523	1262	1912	8170	3967	4879	2232	1114	460
Eurytemora affinis –adults and juveniles	17	44	963	47	115	4	1109	105	52	28
Epischura lacustris –adults and juveniles	–	–	158	–	–	–	–	–	–	–

and declined in the summer in lakes Huron and Ontario, but the proportion of net phytoplankton was highest in the summer in Lake Erie (Table 5).

There were considerable differences in concentrations of ash-free biomass between lakes and regions in lakes, between littoral and pelagic regions in Lake Ontario, between the three basins of Lake Erie and between Saginaw Bay and the main portion of Lake Huron (Fig. 2). Peak values of 1100 mg/m^3 and 800 mg/m^3 were found in the Western Basin of Lake Erie and Saginaw Bay. The pelagic regions of lakes Ontario and Huron generally had the lowest biomass values.

Discussion

Considerable changes in abundance of crustacean zooplankton and in net plankton biomass were found on a yearly basis during sampling seasons extending from April or earlier to December on lakes Huron, Erie, and Ontario. Changes in net biomass were due to changes in species composition and total numbers of crustaceans as well as to changing quantities of net phytoplankton.

Numbers/m^3 for the main lake portion of Lake Huron were lower than those for Lake Ontario, but net biomass values were equal to or greater than those for the open waters of Lake Ontario because of the larger average size of organisms and differing amounts of net phytoplankton present in the samples from the two lakes over the sampling period.

Although concentrations of crustaceans and biomass were highest in inshore waters in all three lakes, there was also a tendency for values for these areas to fluctuate more than those for the offshore areas, especially the main portion of Lake Huron. Fluctuations in numbers of crustaceans can be related in large part to seasonal cycles of short-lived cladocerans and cyclopoid copepods, many

TABLE 3. Mean concentrations (numbers/m^3) of crustacean zooplankton (14 stations, one haul from upper 50 m at each) for 8 cruises on Lake Huron in 1970.

Species	19–27 IV	17–24 V	21–28 VI	19–23 VII	23–30 VIII	28 IX –4 X	27 X –3 XI	29 XI –6 XII
Bosmina longirostris	–	50	150	1020	2120	860	160	65
Eubosmina coregoni	10	–	50	135	770	1155	370	150
Daphnia spp.	–	–	15	50	560	1215	780	95
Holopedium gibberum	–	–	–	85	1135	530	75	5
Polyphemus pediculus	–	–	–	–	45	15	–	–
Ceriodaphnia lacustris	–	–	–	5	+	–	–	–
Diaphanosoma leuchtenbergianum	–	–	–	–	–	5	–	–
Chydorus sphaericus	–	5	–	–	–	125	10	–
Diacyclops bicuspidatus thomasi–adults	190	425	600	265	830	285	125	25
Diacyclops bicuspidatus thomasi–juveniles	475	300	1575	1305	5630	7345	5430	5315
Acanthocyclops vernalis–adults	–	–	–	–	–	+	+	–
Acanthocyclops vernalis–juveniles	5	–	–	–	–	10	20	25
Mesocyclops edax–adults	–	–	–	–	–	15	5	–
Mesocyclops edax–juveniles	–	–	–	–	–	15	5	–
Tropocyclops prasinus mexicanus–adults	5	5	–	+	65	190	70	130
Tropocyclops prasinus mexicanus–juveniles	–	–	–	–	30	5	5	+
Limnocalanus macrurus–adults	15	10	25	55	70	140	15	–
Limnocalanus macrurus–juveniles	5	50	40	10	30	10	–	40
Diaptomus sicilis–adults	150	120	115	110	65	20	145	210
Diaptomus oregonensis–adults	90	60	115	35	85	35	155	295
Diaptomus minutus–adults	675	620	425	310	810	45	110	700
Diaptomus siciloides–adults	40	20	50	–	–	–	10	20
Diaptomus ashlandi–adults	515	360	375	215	85	15	10	395
Diaptomus cops	140	215	720	7225	1160	8720	3470	1310
Eurytemora affinis–adults and juveniles	–	5	20	10	20	–	–	–
Epischura lacustris–adults and juveniles	–	–	–	–	–	25	20	–

TABLE 4. Estimated values (mg/m³) of crustacean biomass, net plankton biomass (ash-free dry weight), and net chlorophyll for the three lakes. Values weighted on a surface-area basis.

	Lake Ontario 1970				Lake Erie 1970				Lake Huron 1971		
Date	Crustacean biomass calculated mg/m³	Ash-free dry weight mg/m³	Net chlorophyll mg/m³	Date	Crustacean biomass calculated mg/m³	Ash-free dry weight mg/m³	Net chlorophyll mg/m³	Date	Crustacean biomass calculated mg/m³	Ash-free dry weight mg/m³	Net chlorophyll mg/m³
Jan. 6–20	9.9	21.6	1.84								
Feb. 3–8	15.7	19.4	1.32								
Mar. 3–8	14.3	67.2	0.98								
Mar. 31–Apr. 4	12.6	54.8	1.66	Apr. 7–11	43.7	86.2	0.67				
Apr. 28–May 1	24.8	90.8	0.91	May 6–10	33.3	191.4	0.23	Apr. 19–27	12.5	64.1	0.48
May 25–29	21.5	76.0	0.47	June 2–6	341.7	431.6	0.06	May 17–24	12.3	94.0	0.45
June 22–27	27.3	66.0	0.32	July 3–7	534.8	360.5	0.24	June 21–28	32.4	93.0	0.36
July 16–20	55.0	127.8	0.22	July 28–Aug. 1	458.0	539.6	1.41	July 19–23	57.7	99.3	0.21
Aug. 17–21	156.9	83.4	0.08	Aug. 25–29	153.9	328.9	1.49	Aug. 23–30	116.3	89.0	0.26
Sept. 14–19	112.0	124.0	0.47	Sept. 23–27	161.3	266.9	2.01	Sept. 28–Oct. 4	96.9	70.1	0.23
Oct. 13–17	106.3	88.2	0.44	Oct. 21–25	61.8	105.5	0.59	Oct. 27–Nov. 3	44.8	63.2	0.36
Nov 16–20	42.3	36.4	0.21	Nov. 25–30	58.1	78.4	0.40	Nov. 29–Dec. 6	32.9	31.0	0.49
Dec. 7–11	19.0	19.0	0.13	Dec. 14–18	32.4	52.0	0.26				

of which seem to have summer maxima, whereas areas with populations largely of calanoids have more stable numbers. Fluctuations in biomass seem to be also related to pulses or blooms of phytoplankton. The pattern of biomass values in the littoral waters of Lake Ontario is very similar at least in the winter and spring months to the abundance of filamentous diatoms found by Munawar and Nauwerck (1971). This paper confirms the finding of Patalas (1972) of midsummer maxima of numbers, species richness, and biomass in the three lakes. However, considerable differences in timing of maxima are evident between the lakes and the littoral and pelagic portions of each.

TABLE 5. Cruise mean net chlorophyll as a percent of total surface chlorophyll for lakes Ontario and Erie in 1970 and Lake Huron in 1971 (total chlorophylls from Glooschenko et al. 1972, 1973, and 1974 article(s) in this issue).

Lake Ontario		Lake Erie		Lake Huron not Saginaw Bay	
Jan. 6–20	22.4				
Feb. 3–8	5.4				
Mar. 3–8	25.7				
Mar. 31–Apr. 4	38.1	Apr. 7–11	3.4		
Apr. 28–May 1	13.1	May 6–10	13.7	Apr. 19–27	44.7
May 25–29	8.9	June 2–6	1.6	May 17–24	21.6
June 22–27	5.7	July 3–7	10.7	June 21–28	10.0
July 16–20	4.0	July 28–Aug. 1	34.6	July 19–23	6.2
Aug. 17–21	2.4	Aug. 25–29	29.9	Aug. 23–30	6.7
Sept. 14–19	8.4	Sept. 23–27	19.8	Sept. 28–Oct. 4	5.0
Oct. 13–17	8.2	Oct. 21–25	8.4	Oct. 27–Nov. 3	13.8
Nov. 16–20	5.3	Nov. 25–30	8.4	Nov. 29–Dec. 6	19.6
Dec. 7–11	5.0	Dec. 14–18	5.3		

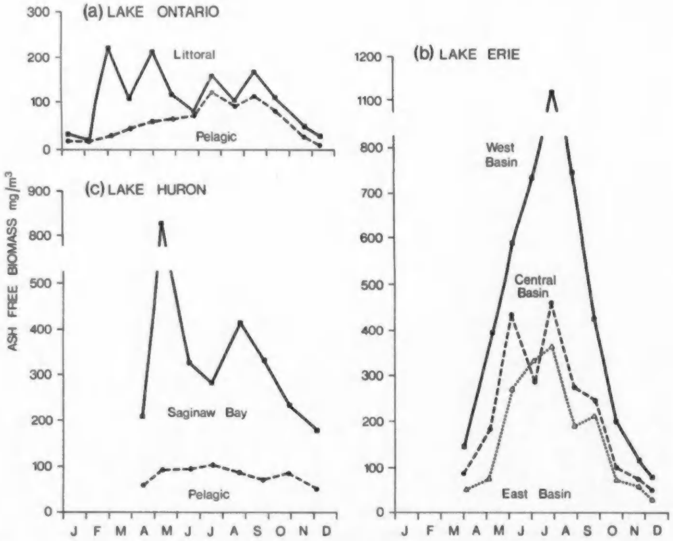

FIG. 2. Plankton net biomass in the littoral and pelagic zones of Lake Ontario (a), the three basins of Lake Erie (b), and the main lake and Saginaw Bay regions of Lake Huron (c).

Acknowledgments

This study was initiated under the guidance of Dr R. A. Vollenweider, whose continued interest is acknowledged. Dr A. Nauwerck was directly involved with the zooplankton study of lakes Ontario and Erie. Mrs L. Devey and Mr S. Metikosh identified and enumerated most of the zooplankton samples.

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Abundance and Life History of *Mysis relicta* in the St. Lawrence Great Lakes

G. F. CARPENTER[1], E. L. MANSEY, AND N. H. F. WATSON

Department of the Environment, Fisheries and Marine Service
Great Lakes Biolimnology Laboratory
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

CARPENTER, G. F., E. L. MANSEY, AND N. H. F. WATSON. 1974. Abundance and life history of *Mysis relicta* in the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 319–325.

In sampling on lakes Ontario, Erie, and Superior during three cruises from spring to fall, and on Lake Huron during eight cruises, *Mysis relicta* was generally not taken or not abundant in waters less than 25 m in depth. Its abundance appeared to increase with depth at least up to 200 m. Populations appeared to be concentrated in waters 125–200 m deep during summer and more dispersed during spring and fall. Highest numbers were found in Lake Superior, followed by lakes Ontario and Huron. A small localized population was found in the deep eastern part of Lake Erie.

Size-frequency distributions from the various cruises on lakes Superior, Huron, and Ontario indicated differences in life cycles of the mysid in the three lakes. In Lake Superior there was one major period of recruitment, from February to July, and the generation time appeared to be 2 yr. In lakes Huron and Ontario recruitment appeared to occur from February to August and to be separated into a winter and a summer period; each of the generations appeared to mature in 18 mo.

CARPENTER, G. F., E. L. MANSEY, AND N. H. F. WATSON. 1974. Abundance and life history of *Mysis relicta* in the St. Lawrence Great Lakes. J. Fish. Res. Board Can. 31: 319–325.

Lors d'échantillonnages effectués dans les lacs Ontario, Erié et Supérieur au cours de trois croisières échelonnées du printemps à l'automne et de huit croisières sur le lac Huron, *Mysis relicta*, en général, n'a pas été capturé ou n'était pas abondant dans des eaux de profondeur moindre que 25 m. Son abondance semble augmenter avec la profondeur, du moins jusqu'à 200 m. Les populations semblent concentrées à des profondeurs de 125–200 m en été, et plus dispersées au printemps et en automne. Elles sont les plus abondantes dans le lac Supérieur, suivi des lacs Ontario et Huron. Nous avons trouvé une petite population isolée dans la partie orientale profonde du lac Erié.

La distribution des fréquences de longueur observées au cours des diverses croisières sur les lacs Supérieur, Huron et Ontario révèle des différences dans le cycle biologique de *Mysis* dans les trois lacs. Dans le lac Supérieur, il y a une période principale de recrutement, de février à juillet, et il semble y avoir un intervalle de 2 ans entre les générations. Dans les lacs Huron et Ontario, le recrutement semble se produire de février à août et se divise en une période d'hiver et d'été; chaque génération semble atteindre la maturité en 18 mois.

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ALTHOUGH there have been many published reports of distribution and vertical migration of the opossum shrimp, *Mysis relicta*, in the Laurentian Great Lakes (Beeton 1960, Foulds 1972), there are few estimates of abundance of this potentially important forage item for fish. Reynolds and DeGraeve (1972) described the life history and abundance of the species in southeastern Lake Michigan.

This study reports on a sampling program for *M. relicta* in the St. Lawrence Great Lakes in 1971. Comparative abundances were obtained for four of the lakes with the same sampling gear on several cruises from spring to fall. Attempts were made to determine life history patterns from size analysis of the catches.

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[1] Present address: Industrial Biotest Laboratories Inc., 1810 Frontage Rd., Northbrook, Ill. 60062, USA.

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Materials and Methods

The mysid was collected from vertical hauls of a net with a 1-m^2 mouth of 505 μ Nitexcloth supported in an aluminum frame. The net was designed so it would rest on its side on the bottom when lowered. This type was selected to sample animals on the bottom (like a benthic sled) and those in the water column. In practice, the net was lowered rapidly to the bottom, the cable was allowed to go slack, and the net was retrieved as a vertical haul.

Samples were collected from 33 stations on eight synoptic cruises of Lake Huron (Fig. 1), from 33 stations on three cruises each of lakes Ontario and Superior (Fig. 2), and from 25 stations on three cruises of Lake Erie (April 15–17, August 17–20, and November 23–26). The ship visited the stations on a predetermined path and sampled day and night, one haul being taken at each station on each cruise. Samples at each station were taken at different times of the day but, in areas of similar depth, no variation in abundance was attributable to differences in time of sampling. On some cruises, because of weather conditions, no samples were taken at up to three stations (Fig. 1,2).

Collections from the net were drained into a large beaker, further concentrated into a collecting bottle, and preserved in 10% formalin. In the laboratory all specimens of the mysid were removed, counted, straightened, and measured to the nearest millimeter from tip of rostrum to tip of telson.

Since males and females smaller than 7 mm in total length were indistinguishable, only those above this size were classified as males and females. The number of females with eggs or embryos was recorded as well. In the size-frequency analyses, adult males were excluded, as they differed from females in either growth or mortality rate.

Results and Discussion

Mysis relicta was not found in the shallow portions of lakes Ontario, Huron, and Superior in the summer and was taken there, in low concentrations, only in the spring and fall (Fig. 1,2). It was collected from only two stations in the eastern end of Lake Erie, on the summer and fall cruises, and must be present in low numbers in this lake.

In Lake Huron (Fig. 1), the mysid was not taken from the southern portion of the lake and Saginaw Bay during most of the summer. It was found in appreciable numbers only at stations deeper than 100 m, in the central and northern portions of the lake associated with areas of deep water.

Mean abundance at the 33 sites sampled in Lake Huron increased from 3.0/m^2 in April to a peak of 60.2/m^2 in June, a second peak of 83.2/m^2 occurring in late September (Table 1). Maximum abundance of 847/m^2 occurred at a station in the northern end of the lake in June (Fig. 1).

In Lake Ontario, the horizontal distribution pattern was similar to that for Lake Huron: the mysid was absent or in low abundance in sampling at either end of the lake and most concentrated in the deeper, central areas (Fig. 2). Abundance was higher than in Lake Huron with a peak average for 30 stations of 112.9/m^2 in August (Table 1). The maximum abundance at a single station (861/m^2) was similar to that in Lake Huron.

The horizontal distribution pattern in Lake Superior was similar to that in the other two lakes. The mysid was not taken or was low in abundance in shallower inshore areas such as Thunder Bay, Nipigon Bay, Whitefish Bay, and areas along the southern shore of the lake. Average abundance at the 33 stations sampled was higher than in Lake Ontario and did not vary appreciably from 155/m^2 (Table 1) during the season. Maximum abundance at a single station (887/m^2) was similar to that in Lake Ontario.

We calculated the relationship between number/m^2 and sampling depth for the 96 samples from Lake Ontario, 227 from Lake Huron, and 96 from Lake Superior. In each case, there was a significant positive correlation between sampling depth and abundance. The equations expressing the relationship were: for Lake Ontario, $y = 1.86x + 24.09$; for Lake Huron, $y = 1.17x + 24.31$; for Lake Superior, $y = 1.60x + 25.13$, where y = depth of sampling station in meters, and x = number/m^2.

Abundance (number/m^2) and concentrations (number/m^3) of the mysid taken in hauls from the various depth zones of the three lakes (Table 2) indicate that abundance increased with depth at least up to 200 m, but the relationship beyond that depth was not clear. Reynolds and DeGraeve (1972) using a bottom sledge reported a similar increase in abundance with depth at least to 150 m in southeastern Lake Michigan.

The relationship of number/m^3 to depth similarly increased to approximately 125 m and remained generally steady (lakes Ontario and Huron) or decreased slightly with depth (Lake Superior). This suggests that many of the mysids we sampled in deep water were in the water column, in a fairly dense band below 125 m and above 200 m.

Direct observations confirming this type of distribution were made by Robertson et al. (1968) from a submarine in Lake Michigan. They found numerous mysids in the water column below 150 m and few above this depth. This tendency for *M. relicta* populations to be distributed partly on the bottom and partly in the water column makes precise population estimates difficult.

The smallest specimens found were 3 mm in total length, the same as found by Reynolds and De-

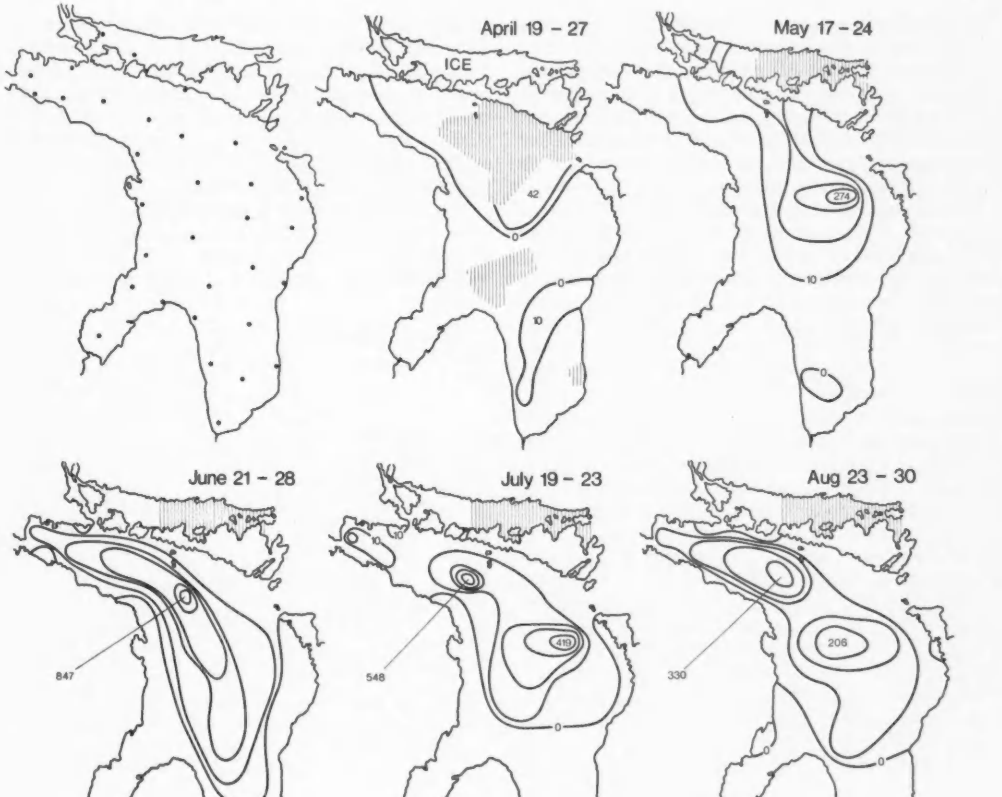
April 19 - 27
ICE
42
0
0
10
May 17 - 24
274
10
0
June 21 - 28
847
0
July 19 - 23
10
10
548
419
0
Aug 23 - 30
330
206
0
Sept 28 - Oct 4
446
579
0
0
93
Oct 27 - Nov 3
175
10
183
0
Nov 29 - Dec 6
133
0
356

FIG. 1. Sampling stations and seasonal distribution pattern (number/m^2) of *Mysis relicta* in Lake Huron, 1971. Isopleths, in succession: 0, 10, 75, 150, 300, and 600/m^2; hatched areas, no samples. A single vertical haul made from bottom at each station on each cruise.

Graeve (1972). Largest females were 21 mm in total length and largest males 17 mm.

Changes in size distribution of females and juveniles <7 mm in total length were apparent from cruise to cruise in lakes Superior, Huron, and Ontario (Fig. 3). If these changes are not artifacts of sampling then they are reflections of growth and development.

During the spring cruise on Lake Superior there appeared to be two major peaks of abundance: for juveniles at 3 mm and females at 10 mm. A month later the modal size of juveniles <7 mm increased to 4 mm whereas that of females remained the same. By October, very few juveniles <5 mm were taken, and the major mode was at 6 mm. A second mode appeared at 12 mm, suggesting growth of the larger group. Egg-bearing females were larger than 12 mm and never made up more than 1% of the total number of females but were most numerous in the late May cruise.

The size-distribution polygons suggest there is a fairly simple life cycle pattern in Lake Superior. Recruitment to the population takes place from spring at least to July, after 1 yr the modal length of

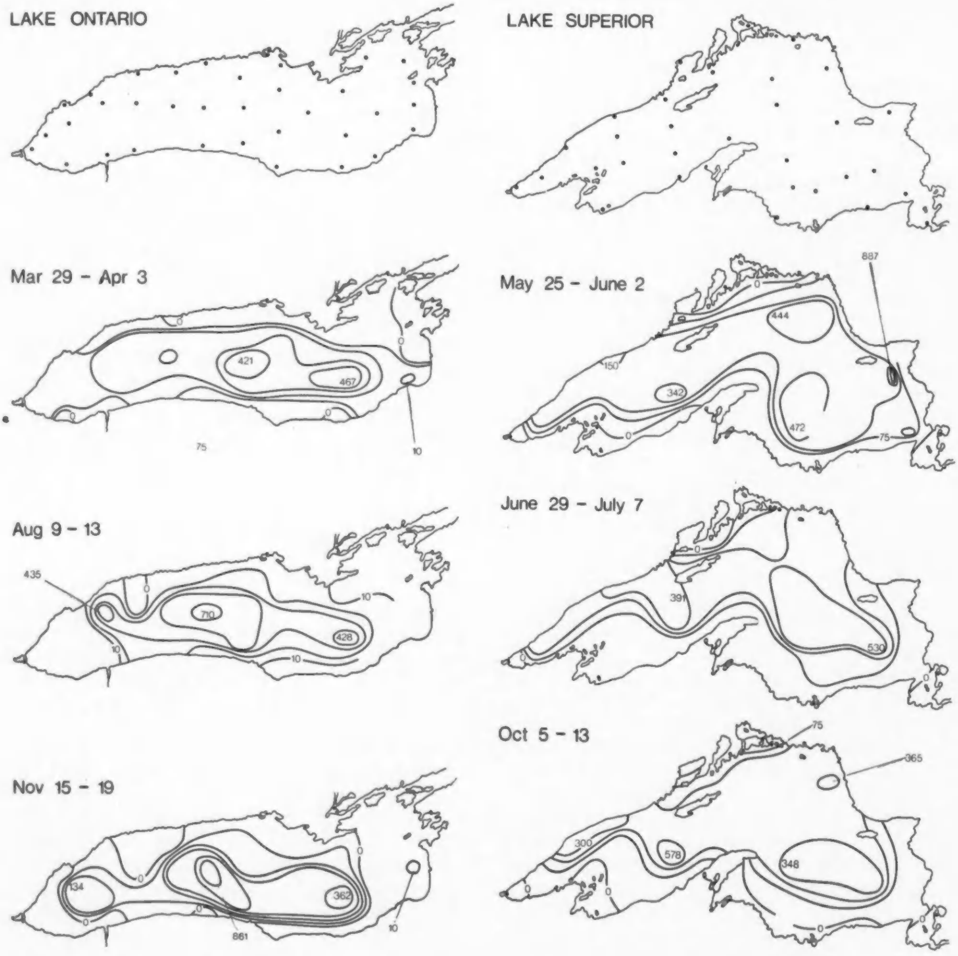
LAKE ONTARIO
Mar 29 - Apr 3
0
421
467
0
0
0
75
10
Aug 9 - 13
435
0
710
10
428
10
10
Nov 15 - 19
134
0
0
362
0
0
861
10
LAKE SUPERIOR
May 25 - June 2
887
0
444
150
342
472
75
0
June 29 - July 7
0
391
530
0
0
Oct 5 - 13
75
365
300
578
348
0
0
0

FIG. 2. Sampling stations and seasonal distribution pattern of *M. relicta* in lakes Ontario and Superior in 1971. Isopleths as in Fig. 1.

animals would be 10 mm, and females would reach maturity (12–15 mm) after 2 yr. Mortality is apparently high considering the relatively high percentages of juveniles in the population.

TABLE 1. Mean number/m^2 of *Mysis relicta* for each cruise (single samples at 25–33 stations) in lakes Ontario, Huron, and Superior, 1971.

Date	No./m^2
Lake Ontario	
Mar. 29–Apr. 3	72.4
Aug. 9–13	112.9
Nov. 15–19	73.5
Lake Huron	
Apr. 19–27	2.9
May 17–24	15.5
June 21–28	60.2
July 19–23	43.6
Aug. 23–30	38.9
Sept. 28–Oct. 4	83.2
Oct. 27–Nov. 3	36.9
Nov. 29–Dec. 6	39.1
Lake Superior	
May 25–June 2	162.2
June 29–July 7	154.7
Oct. 5–13	145.2

In spring and early summer especially there was a much higher percentage of females greater than 15 mm in length in Lake Huron (Fig. 3) than in Lake Superior. There was a considerable percentage of juveniles 3–5 mm in length in the April samples and some 6–8 mm long, the latter being insignificant in the Lake Superior samples in spring and early summer. In April, the female distribution also seemed to be bimodal, with poorly defined peaks of abundance at 10 and 13 mm. Later in the year, the peaks shifted through the size ranges as if they represented the growth of groups of mysids. The peak at 10 mm in April appeared to represent the same group as that at 15 mm in October, and that at 4 mm in April the same as that at 10 mm in October.

The population structure of the mysid in Lake Huron appears considerably more complex than in Lake Superior or southeastern Lake Michigan as described by Reynolds and DeGraeve (1972). In these two situations there appeared to be an extended period of reproduction in winter and spring leading to recruitment of 3-mm juveniles until July. In July in Lake Superior the bulk of the females were under 15 mm in length with only a small percentage of larger forms. In Lake Huron the size-frequency distribution was marked by more modes and a higher percentage of larger forms than that for Lake Superior. The presence of small mysids from April to early October suggested breeding and recruitment from winter until well into fall. This was confirmed by the finding that between 10 and 20% of females examined from

TABLE 2. Abundance (number/m^2) and concentrations (number/m^3) of *M. relicta* in samples taken from different depth zones in lakes Ontario, Huron, and Superior, 1971.

	Number/m^2			Number/m^3		
Depth zone (*m*)	Lake Ontario	Lake Huron	Lake Superior	Lake Ontario	Lake Huron	Lake Superior
0–25	3.70	0.61	1.56	0.14	0.03	0.08
25–50	5.75	13.00	24.28	0.14	0.28	0.59
50–75	33.13	15.00	14.00	0.53	0.24	0.22
75–100	107.67	57.23	117.00	1.15	0.63	1.37
100–125	180.20	97.25	261.00	1.67	0.81	2.33
125–150	121.86	155.15	128.94	1.01	1.14	0.95
150–175	329.80	128.25	284.40	1.79	0.80	1.70
175–200	–	369.00	315.37	–	1.91	1.66
200–225	419.00	198.60	247.57	1.78	0.91	1.15
225–250			287.00			1.20
250–275			472.50			1.76
275–300			–			–
300–325			–			–
325–350			–			–
350–375			–			–
375–400			259.00			0.93

May to July bore eggs or embryos and the percentage with eggs in October, December, and April was less than 1%. The complex size-frequency distribution, with a relatively high proportion of mysids 15 mm or larger in the spring, was considerably different from the pattern evident in Lake Superior. There may be two main periods of reproduction per year: one in winter and early spring and one in early summer. Conversely, the period of reproduction may be considerably longer than in Lake Superior. In any case, there appeared to be two peaks of recruitment per year, so that the size distributions contained more peaks than those for Lake Superior.

The size distributions of the mysids in the Lake Huron samples suggested that recruits entering the population at 3 mm in the spring reached 10–12 mm by the following spring and 15 mm by the next summer, when they were egg-bearing. Those recruited in July and August would be 7 mm by the following spring and 15 mm the following winter when they were 18 mo old.

The size frequency distributions from the three cruises on Lake Ontario (Fig. 3) indicate much the same situations as in Lake Huron. Animals larger than 15 mm made up a considerable percentage of the population. There appeared to be several size-groups in the population. About 5% of the females in November were bearing eggs, suggesting a period of winter reproduction. Recruitment was evident in April and August but not November.

The length of the life cycle and season of reproduction of *M. relicta* seems to vary markedly from lake to lake. Larkin (1948) found that the species took 2 yr to reach maturity in Great Slave Lake and reproduction occurred primarily in winter. More recently, Lasenby and Langford (1972) concluded from trimodal size-frequency polygons that life cycles in Char Lake, N.W.T., and Stoney Lake, southern Ontario, are of 2- and 1-yr duration. Reynolds and DeGraeve (1972) postulated a 1-yr life cycle for the species in southern Lake Michigan. They also noted an extended period of recruitment

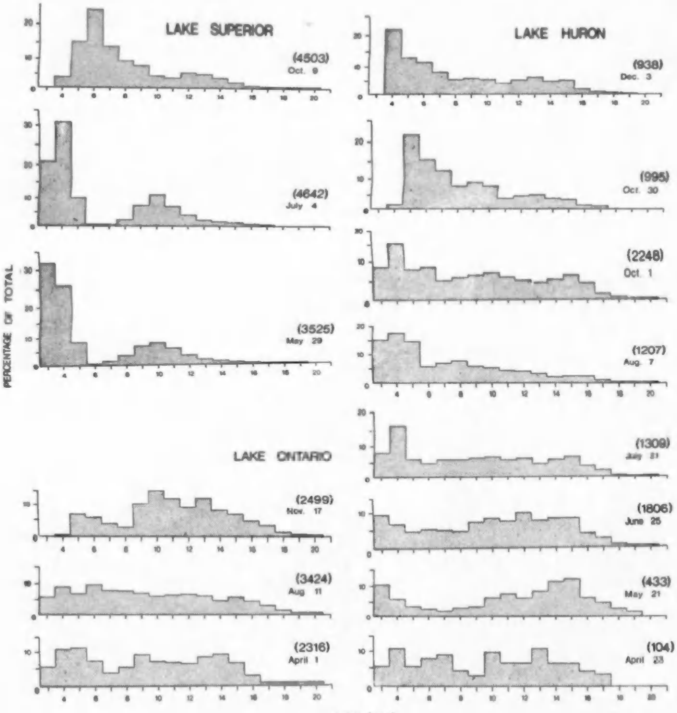

FIG. 3. Size-frequency distribution of *M. relicta* females and juveniles <7 mm for each cruise on three lakes (males excluded because of different growth or mortality rate). Numerals in parentheses are totals taken.

from April to November. Their size-frequency data resemble those from Lake Superior more closely than those from Lake Huron. Fürst (1972) suggested that in some lakes in Sweden there may be two populations living together but separated by different breeding times. Our preliminary analysis of the Lake Huron populations indicates that a summer breeding population gives rise to a winter breeding one and vice versa. However, further sampling and analysis is necessary to elucidate the duration of the breeding season and possible existence of separate populations in the lakes.

Acknowledgments

The advice and direction of Drs R. A. Vollenweider and A. Nauwerck in the design and carrying out of the sampling program is gratefully acknowledged. Samples were collected by the technical operations crew of the MV *Martin Karlsen* and Messrs R. H. Collins, J. E. Moore, J. K. Leslie, and S. Metikosh. We would also like to acknowledge the constructive criticism of the manuscript by Drs J. Reynolds and J. Roff.

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A Proposed Method Suitable for Large-Scale Surveys of Biomass in Lakes

GEORGE F. CARPENTER[1]

Department of the Environment
Fisheries and Marine Service, Great Lakes Biolimnology Laboratory
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

CARPENTER, G. F. 1974. A proposed method suitable for large-scale surveys of biomass in lakes. J. Fish. Res. Board Can. 31: 327–328.

A method for studying plankton biomass by comparing the results between planktonnet hauls and an integrated water column sample is described. Filtering the planktonnet sample through glass-fiber filter papers would yield planktonnet phytoplankton plus zooplankton biomass. Filtering the integrator sample would yield total phytoplankton biomass. Sieving part of this sample would give direct estimates of net and nannophytoplankton which could be used in combination with the values of net plankton biomass to give estimates of total biomass and zooplankton biomass.

Ash-free dry weight is recommended instead of dry weight biomass. The results are easy to produce, are comparable with other parameters such as particulate carbon and nitrogen, and are in units which may be used in the determination of trophic status or nutrient budgets for a lake.

CARPENTER, G. F. 1974. A proposed method suitable for large-scale surveys of biomass in lakes. J. Fish. Res. Board Can. 31: 327–328.

L'auteur décrit une méthode pour étudier la biomasse du plancton en comparant les résultats de l'échantillonnage du plancton au filet avec un échantillon intégré de la colonne d'eau. Le filtrage de l'échantillon du filet à plancton à travers des papiers-filtres en fibre de verre donnerait le phytoplancton du filet, plus la biomasse du zooplancton. Le filtrage de l'échantillon de l'intégrateur donnerait la biomasse totale du phytoplancton. Le tamisage d'une partie de cet échantillon donnerait des estimés directs du phytoplancton du filet et du nannophytoplancton, valeurs qui pourraient être combinées avec celles de la biomasse nette du plancton pour donner des estimés de la biomasse totale et de la biomasse du zooplancton.

On recommande l'emploi du poids sec moins les cendres au lieu du poids sec de la biomasse. Les résultats sont faciles à obtenir, sont comparables avec les autres paramètres tels le carbone particulaire et l'azote, et se présentent en unités qui peuvent être utilisées dans la détermination de l'état trophique ou des budgets en substances nutritives d'un lac.

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THE purpose of this note is to elaborate on the biomass methods described by Watson and Carpenter (1974) and to show how they may be useful in routine plankton surveys or monitoring of large lakes. Vertical planktonnet hauls were taken through the upper 50 m of the water column and separated into three portions. One portion was used for microscopic identification and counting of zooplankton, the results of which were also converted to biomass estimates using mass values determined separately for each major taxon or species. The other two portions were used to make direct measurements of chlorophyll *a* and dry weight and ash-free dry weight.

Biomass estimates based on microscope counts are slow to prepare and may be biased by both the accuracy of these counts and the seasonal variability of conversion factors which must be continually recalculated. Total dry weight measurements may include much inorganic sediment in inshore areas or resuspended dead organic material. No distinction between phytoplankton, zooplankton, and organic detritus is possible using either dry weight or ash-free dry weight estimates (the proportions of which may change between sampling periods and locations). The relationship between chlorophyll *a* and phytoplankton biomass is also variable and

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[1] Present address: Biotest Laboratories Inc., 1810 Frontage Road, Northbrook, Ill. 60062, USA.

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poorly defined. Despite these inherent problems, biomass estimates have the very real advantage in that they are easily produced, are easily compared or converted to other parameters such as total particulate carbon, nitrogen, or phosphorus and are in units which may be used in the determination of trophic status or nutrient budgets.

In the study described, the ratios of nanno- to planktonnet phytoplankton were estimated from chlorophyll *a* measurements. Because of the difficulty in relating chlorophyll *a* to biomass, no estimates of phytoplankton biomass were attempted and therefore the separation of biomass into phytoplankton and zooplankton fractions was not possible.

Our experience suggests that the analysis of two samples at each station for biomass would provide this information. These samples would come from a vertical planktonnet haul and a water sample collected to the same depth with a sampler which integrates the water column, such as that described by Schröder (1969). Replicate samples or composited samples would be desirable. Portions of the samples may also be preserved for other analyses.

Filtering the planktonnet haul through glass-fiber filters would yield planktonnet phytoplankton plus zooplankton biomass while the integrated water sample would yield estimates of phytoplankton biomass including nannoplankton. By passing a portion of the integrated sample through a sieve of mesh size comparable to the net, a measurement of nannoplankton biomass would be obtained which would be more accurate than that obtained by calculating the difference between the total biomass derived from the integrator and the net plankton biomass derived from the net hauls. Since the integrator is not likely to sample the larger free-swimming zooplankton quantitatively because of their lower densities and ability to escape the intake valve, this sample will give a biomass value closely resembling phytoplankton biomass, especially if the occasional large zooplankters are picked off (Robertson and Powers 1967).

The size of samples obtained by these two collecting methods is adequate for portioning into several subsamples which may be preserved for several types of analyses such as microscope counts, analyses for dry weight, ash-free dry weight or particulate elements, and chlorophyll *a* measurements as mentioned earlier. More important, however, this comparison of two types of samples provides a simple solution to the problem of separating the major categories of seston for rapid routine analysis, the results of which are adequate for monitor or survey studies after original detailed studies have been completed for a lake.

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Exchange of Carbon Dioxide Between the Atmosphere and Lake Ontario

R. R. WEILER

Department of the Environment, Fisheries and Marine Service
Great Lakes Biolimnology Laboratory
Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

WEILER, R. R. 1974. Exchange of carbon dioxide between the atmosphere and Lake Ontario. J. Fish. Res. Board Can. 31: 329–332.

The calculated flux of carbon dioxide between Lake Ontario and the atmosphere ranged from about 0.1 gC m^{-2} day^{-1} during the summer to about 3 during a winter storm. During the summer, the amount of carbon supplied from the atmosphere was from 5 to 30% of the estimated amount utilized in primary production. Also Lyman's dissociation constants for carbonic acid were found applicable to the carbonate system of the lake.

WEILER, R. R. 1974. Exchange of carbon dioxide between the atmosphere and Lake Ontario. J. Fish. Res. Board Can. 31: 329–332.

Le flux de CO_2 calculé entre le lac Ontario et l'atmosphère varie d'autour de 0.1 g C m^{-2} $jour^{-1}$ en été à autour de 3 pendant les tempêtes d'hiver. En été, la quantité de carbone fournie par l'atmosphère est de 5 à 30% des estimés utilisés dans la production primaire. On démontre également que les constantes de dissociation de Lyman pour l'acide carbonique sont applicables au système des carbonates du lac.

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THIS report is the first from a long-term study on the air–water exchange of carbon dioxide on the Great Lakes. The variation of carbon dioxide partial pressure in the air ($P\text{co}_2$)over Lake Ontario was measured at intervals from July 1972 to March 1973. The flux of CO_2 between lake and atmosphere was obtained from the difference between $P\text{co}_2$ and the calculated partial pressure in the lake ($p\text{CO}_2$) multiplied by the transfer coefficient for CO_2, which varies with wind speed (Kanwisher 1963; Hoover and Berkshire 1969; Liss 1973). Since $p\text{CO}_2$ depends on the particular dissociation constants for carbonic acid used, applicability of the Lyman values was tested by comparing the measured and calculated total inorganic carbon contents of lake water.

Methods — The $P\text{co}_2$ was measured during five cruises (middle dates in Table 1). During each cruise, lasting 5 days, four north–south transects of the lake were made. Also, the ship was stopped from 12 to 30 h at a station (43°35′24″N, 78°00′42″W) in the middle of the lake.

The air intake was located at the top of the foremast. After drying with $MgClO_4$ and filtering, the air was passed through a UNOR-2 nondispersive infrared analyzer, where the $P\text{co}_2$ was compared with that of known reference gases. The precision of the measurements was about ± 1 ppm.

While at station, the water column was sampled at around 0800, 1900, and at 0500 the following day. The alkalinity, *p*H, temperature, and total inorganic carbon were determined. From these, the partial pressure of CO_2 in the lake was calculated. The *p*H values were measured within 10 min of the sampling

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TABLE 1. Calculated fluxes of CO_2 between air and water for daylight (about 0900–1900) and night (1900–0500) periods at midlake station on five dates.

Date		Wind speed (m/s^{-1})	Flux ($gC\ m^{-2}day^{-1}$) Line A	Line B
July 19, 1972	Day	2.5	0.64	0.07
	Night	0.4	0.51	0.05
Sept. 7	Day	5.3	0.37	0.14
	Night	3.3	0.39	0.07
Oct. 19	Day	4.4	–0.50	–0.15
	Night	4.1	–0.50	–0.14
Jan. 10, 1973	Day	15.5	–3.0	–1.9
Mar. 7	Day	8.9	–2.7	–2.1

and were accurate to about ± .05 pH units. The alkalinity was measured colorimetrically on an Autoanalyzer with an accuracy of about ± 0.7 ppm. The total inorganic carbon was measured by an adaptation of Swinnerton's et al. (1962) gas-chromatographic method with an estimated accuracy of ± 1%.

The equation used for calculating pCO_2 was:

$$pCO_2 = (A/\alpha_0)\,(a_{H+}/K'_1)\,(1/(1 + 2\,K'_2/a_{H+}))$$

where K'_1 and K'_2 are the apparent dissociation constants for carbonic acid, α_0 is the solubility of CO_2 in distilled water, $a_H = 10^{-pH}$ and A is the alkalinity. K'_1 and K'_2 are Lyman's 1956 values as given by Riley and Skirrow (1965) and corrected as discussed below. α_0 is from Murray and Riley (1971). The calculations were done at the in situ temperature.

The measured total inorganic carbon values (ΣCO_2) were compared with the calculated ones for a cruise on October 16–20, 1972, using the equation

$$\Sigma CO_2 = A(1 + K'_2/a_{H+} + a_{H+}/K'_1)\ /\ (1 + 2K'_2/a_{H+})$$

The formula used for calculating the flux (Kanwisher 1963) was

$$F = (D/h)\cdot \Delta P \cdot \alpha$$

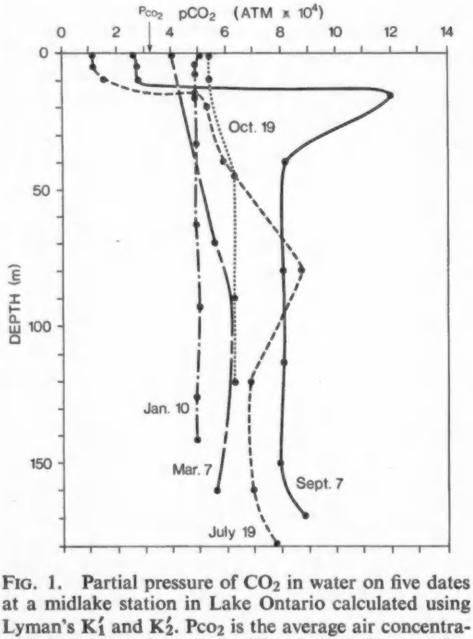

FIG. 1. Partial pressure of CO_2 in water on five dates at a midlake station in Lake Ontario calculated using Lyman's K'_1 and K'_2. P_{CO_2} is the average air concentration for the study periods. The thermocline was between 10 and 20 m.

where F is the flux in moles $cm^{-2}\ s^{-1}$; α is the solubility (moles $l^{-1}\ atm^{-1}$); D is the diffusivity ($2.10^{-5}\ cm^2 s^{-1}$), $\Delta P = P_{CO_2} - pCO_2(atm)$ and h (cm) the thickness of an assumed film which acts as a primary barrier to gas transfer.

Calculation of pCO_2 and its distribution in the lake — In addition to Lyman's constants, a correction to K'_1 for the effect of ionic strength (Hoover 1966) and an alternative value for K'_2 (Takahashi et al. 1970), were used to calculate ΣCO_2. The differences (δ) between the calculated and measured values for these three conditions were:

Lyman's K'_1	0.60±1.45
Hoover's K'_1 (A)	0.35±1.45
(A) and $K'_2 = 1.3 \times (K'_2)$ Lyman	0.21±1.45

where δ is $(((\Sigma CO_2)_{calc}/(\Sigma CO_2)_{meas}) - 1) \times 100$

and the variation is $\pm\sigma$. The ionic strength was taken as 0.005.

As can be seen, use of both corrections decreased the difference between the calculated and measured values. However, the average δ using Lyman's constants was within experimental error. Certainly the empirical constants suggested by Wood and Verduin (1972) for Lake Erie are not applicable to Lake Ontario.

The choice of constants had a greater effect on pCO_2 than on ΣCO_2, since values calculated using both corrections were about 13% lower than those calculated using Lyman's K'_1 and K'_2.

During summer, the pCO_2 (Fig. 1) above the thermocline, which lay between 10 and 20 m, was less than the air equilibrium value (P_{CO_2}). It increased at the thermocline and decreased again to a value about twice

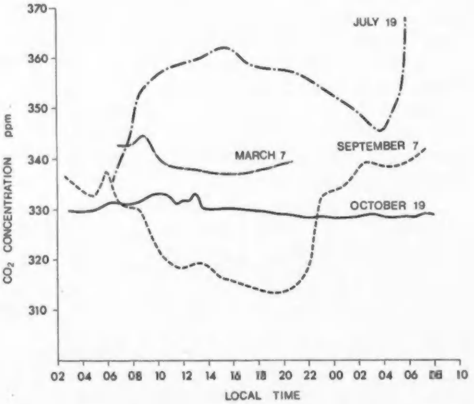

FIG. 2. Concentration of CO_2 in air at the midlake station on four dates. The units are ppm by volume for a dry atmosphere.

the air equilibrium. In the winter, the pCO_2 was relatively uniform from top to bottom and approached the air equilibrium as the lake was mixed by winter storms. Thus, in the summer, the lake acts as a sink; in the winter, as a source of CO_2.

Pco_2 measurements — Of special interest is the September curve for concentration of CO_2 in the air at the midlake station (Fig. 2), as it reflects the photosynthetic activity on the land surrounding the lake and possibly in the lake. The midday peak for the July curve was likely caused by industrial activity in northeastern United States, since, at that date, the weather was dominated by a large-scale flow of air from the south.

Carbon dioxide flux — The model used in calculating the carbon dioxide flux (Fig. 3) assumes that a thin, laminar film exists at the air–water interface. The gas passes through it by molecular diffusion and is mixed

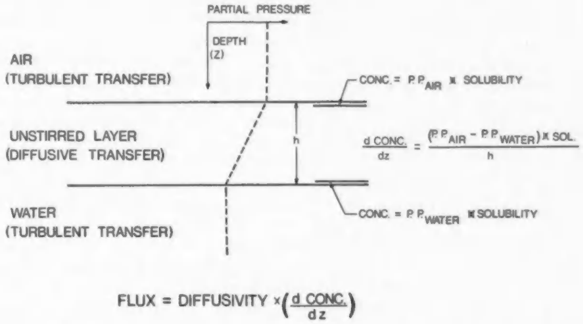
PARTIAL PRESSURE
DEPTH (Z)
AIR (TURBULENT TRANSFER)
CONC. = P.P.AIR × SOLUBILITY
UNSTIRRED LAYER (DIFFUSIVE TRANSFER)
h
d CONC./dz = (P.P.AIR − P.P.WATER) × SOL./h
WATER (TURBULENT TRANSFER)
CONC. = P.P.WATER × SOLUBILITY
FLUX = DIFFUSIVITY × (d CONC./dz)

FIG. 3. Model (Kanwisher 1963) used for calculating carbon dioxide fluxes.

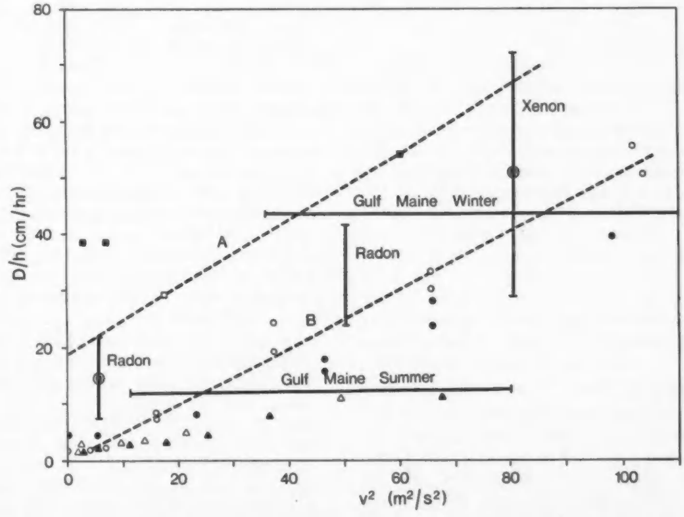

FIG. 4. Variation of the transfer coefficient for carbon dioxide (D/*h*) with wind speed. Wind tunnel measurements by Kanwisher (1963) are shown as ○ for a smooth water surface and ● for a surface with waves; by Hoover (1966) as △; and by Liss (1973) as ▲. Field measurements by Park and Hood (1963) are shown as □ and by Sugiura et al. (1963) as ■. The five other field measurements, designated by labelled solid lines, are from Schink et al. (1970).

into the water by turbulent diffusion. Since the film is very thin, the concentration is assumed to vary linearly across it.

Figure 4 summarizes published wind tunnel and field measurements of the transfer coefficient D/*h* (cm h^{-1}) for CO_2. The coefficient varies linearly with the square of the wind velocity. The differences between the field measurements and the laboratory ones, which were lower than the former, are as yet unexplained, but, since the exchange of CO_2 is principally controlled by resistance (inverse of transfer coefficient) of the liquid phase (Liss 1973), it must be connected with differences in the turbulence regimes in the lakes and in the laboratory setups. Although some recent results by Atkinson (1972) are even higher, the lines A and B in Fig. 4 represent the probable upper and lower ranges of D/*h*, since they agree with some field results of Teal and Kanwisher (1966). They estimated, from the increase of pCO_2 during a storm, a value of 300 cm h^{-1} for D/*h* for V = 22 m s^{-1}. By extrapolation to this V, the lines labelled A and B give D/*h* values close to 300, namely 304 and 251, respectively.

The average fluxes for daylight and night periods while the ship was on station (Table 1) were calculated using both lines A and B. For each period, values were averaged for pCO_2, using corrected K_1' and K_2' values; P_{CO_2}, corrected for relative humidity; and wind speed. The fluxes ranged from a low of 0.1 gC m^{-2} day^{-1} in July to a high of 3 during the winter months when the lake was degassing during a storm. The fluxes obtained for low wind speeds fall in the range (0.2 gC m^{-2} day^{-1}) found by Schindler et al. (1972) for a small protected lake near Kenora, Ont.

During July and September, when primary production was approximately 1.2 gC m^{-2} day^{-1} (personal communication, P. Stadelmann, Canada Centre for Inland Waters), the amount of carbon supplied from the atmosphere was from 4 to 53% of the amount utilized. As a consequence, the total inorganic carbon in the surface layers during summer should be less than during winter. This is borne out by our results. In July, ΣCO_2 was 1.7–1.8 mM/liter whereas in March it was 1.85–1.9.

Conclusions — Lyman's K_1' and K_2' values can be used to calculate ΣCO_2 to ± 1% in Lake Ontario.

The calculated CO_2 fluxes between the lake and the atmosphere support the conclusion of Verduin (1956) that respiration and photosynthesis in aquatic environments similar to those of the Great Lakes are in a steady-state relationship and the slow CO_2 exchange between lake and water make it approximate a closed system with respect to CO_2.

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NOTES

Long-Chain Monoethylenic and Other Fatty Acids in Heart, Liver, and Blubber Lipids of Two Harbor Seals (*Phoca vitulina*) and One Grey Seal (*Halichoerus grypus*)

R. G. Ackman and S. N. Hooper

Department of the Environment
Fisheries and Marine Service, Halifax Laboratory, Halifax, N.S.

Ackman, R. G., and S. N. Hooper. 1974. Long-chain monoethylenic and other fatty acids in heart, liver, and blubber lipids of two harbor seals (*Phoca vitulina*) and one grey seal (*Halichoerus grypus*). J. Fish. Res. Board Can. 31: 333–341.

The fatty acids of triglycerides in the hearts from two harbor seals (*Phoca vitulina*) and one grey seal (*Halichoerus grypus*) differed quantitatively in some details from those in the blubber. The 22:1 found in the heart triglycerides was about half that in the blubber triglycerides. Isomer distributions differed within 20:1 acids in the two triglycerides for both species, the higher proportion of 20:1ω11 fatty acid deposited in the heart than in the blubber indicating more active chain shortening from 22:1. The fatty acids of phospholipids of all three hearts and livers also differed quantitatively in some fatty acid details indicating organ-specific compositions. These also differed from compositions of similar lipids in terrestrial animals in their generally marine fatty acid compositions which were established for the blubbers. The grey seal (age 3 mo) showed unusual percentages of linoleic types of acids in the organ lipids and also a curious enrichment in ω7 monoethylenic acids. Dietary factors are believed to be responsible for differences between this animal and the two harbor seals (ages 10 and 23 mo).

Ackman, R. G., and S. N. Hooper. 1974. Long-chain monoethylenic and other fatty acids in heart, liver, and blubber lipids of two harbor seals (*Phoca vitulina*) and one grey seal (*Halichoerus grypus*). J. Fish. Res. Board Can. 31: 333–341.

Les acides gras des triglycérides dans le coeur de deux phoques communs (*Phoca vitulina*) et d'un phoque gris (*Halichoerus grypus*) diffèrent quantitativement par certains détails de ceux du lard. Le 22:1 observé dans les triglycérides du coeur est la moitié environ de celui des triglycérides du lard. La répartition des isomères est différente dans les acides 20:1 des triglycérides des deux espèces, la plus forte proportion d'acide gras 20:1ω11 déposé dans le coeur comparativement au lard indiquant un raccourcissement plus actif à partir de 22:1. Les acides gras des phospholipides des trois coeurs et foies diffèrent quantitativement aussi par certains détails, ce qui indique une composition spécifique à l'organe. Ils diffèrent également des lipides semblables présents chez les animaux terrestres par la composition de leurs acides gras, généralement marins, qui ont été déterminés pour le lard. Le phoque gris (âgé de 3 mois) montre des pourcentages anormaux de types linoléiques d'acides dans les lipides des organes de même qu'un enrichissement singulier en acides ω7 monoéthyléniques. A notre avis, des facteurs du régime alimentaire sont responsables des différences observées entre le phoque gris et les deux phoques communs (âgés de 10 et 23 mois).

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Laboratory studies have shown that in weanling rats and juvenile animals of some other species a continuous exposure to high dietary concentrations of docosenoic acids (i.e. C_{22} chain length, one ethylenic bond; shorthand notation 22:1) leads to temporary lipidosis (fatty deposits) in the cardiac muscle. This condition normally regresses in the rat but later (a convenient experimental period in the male rat is 16 wk) necrotic lesions may appear.

No specific hazard to human health is indicated by these laboratory experiments with animals, but as a precautionary measure limitation of the docosenoic acid content of edible fat and oil products to a maximum of 5% has been implemented in

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Canada (Anon 1973). This measure was designed to reduce consumption of 22:1 from edible oils and fats, including rapeseed oils, partially hydrogenated rapeseed oils, and partially hydrogenated marine oils. In 1972 these marine oils comprised about 5% of the total fats refined for edible use in Canada (B. Weinberg personal communication). Other animal species and age-groups may respond differently, for example by depositing 22:1 more gradually in heart lipid (Rocquelin et al. 1973). Literature reports of scientific experiments in which marine oils (partially hydrogenated or natural) are cited include: Astorg and Rocquelin 1974; Beare-Rogers and Nera 1972; Beare-Rogers et al. 1971, 1972a, b; Conacher et al. 1973; Lang and Reimold 1971; Odense and Brockerhoff 1971; Tiege and Beare-Rogers 1973; Ziemlanski et al. 1972a, b, c. These include important discussion and references to work not including marine oils but based mostly on rapeseed oils, where controversial viewpoints on this whole problem remain to be resolved by further research (Staron and Moreau 1972; Rocquelin et al. 1973).

One aspect which has received little attention is study of the results of ingestion of docosenoic acid and eicosenoic (C_{20}, one ethylenic bond; shorthand notation 20:1) by larger animals as part of a normal diet. Among the animals receiving these fatty acids on an irregular or continuous basis are the seals. As only one report has been published on seal heart lipids (on one animal, Ackman et al. 1972) we have examined lipids and fatty acids of the hearts of three seals of different ages (one grey seal aged 3 mo, two harbor seals aged 10 and 23 mo), and compared details with liver phospholipids and blubber triglyceride fatty acids to determine if deposition of the 20:1 and 22:1 acids occurs in any established pattern. Apparently the levels of these particular fatty acids in cardiac triglycerides are related to those in the blubber and they are normal components of seal heart lipids.

Materials and methods — Two harbor seals were shot near Sambro, Nova Scotia at the times indicated in Table 1. A grey seal was recovered drowned from a fisherman's net near Sambro. As far as could be determined by visual examination at autopsy these were normal healthy animals. Identification as harbor seals (*Phoca vitulina*) and a grey seal (*Halichoerus grypus*) and ages were provided through the courtesy of the Arctic Biological Station, Fisheries and Marine Service, Ste. Anne de Bellevue, Quebec. Within a few hours of death heart, liver, and blubber samples were taken from each. Liver and blubber were stored frozen at –40 C for later study. Whole hearts were extracted at once by the method of Bligh and Dyer (1959). Livers were later trimmed of exposed surface and about 100 g extracted and treated similarly to heart lipids. Blubber (approximately 10 g) was extracted by the method of Bligh and Dyer (1959) with addition of water. All operations were carried out with solvents redistilled in glass and under nitrogen atmosphere. Approximately 0.5 g of organ lipid was applied to a column of Dow Chemical Co. styrenedivinylbenzene copolymer beads (Sipos and Ackman 1968; Drozdowski and Ackman 1969) and eluted with benzene. A polar lipid fraction, considered to be mostly phospholipids, eluted first followed by triglycerides (Table 1). Fraction purity was monitored by thin layer chromatography.

The depot fat was saponified and nonsaponifiable matter was removed with diethyl ether. The fatty acids recovered after acidification were converted to methyl esters by refluxing for 10 min with 7% BF_3 in methanol. Organ lipid fractions were transesterified with the same reagent by refluxing for 30 min. Aliquots of all methyl esters were hydrogenated. Gas–liquid chromatography of methyl esters was carried out on wall-coated open-tubular capillary columns (stainless steel), 46 m (150 ft) in length and 0.25 mm (0.01 inch) ID operated in a Perkin-Elmer Model 990 gas–liquid chromatograph as described elsewhere (Ackman et al. 1967). Two decimal places (Table 2) are solely to show minor components. Actual accuracy should be within ± 5% for major (>10%) components, ± 10% for moderate (1–10%) components, and ± 50% for minor (<1%) components. A mixture including the dimethyl acetals of tetradecanal and hexadecanal was run under the same conditions to determine accurately the positions of acetal breakdown products (Ackman 1972) which account for most of the "unknown" gas–liquid chromatography peaks summed in Table 2.

Another harbor seal was collected but was found to show abnormalities in internal organ condition and results are not included, although the blubber fatty acid composition resembled that of the grey seal.

Results — Blubber triglycerides — In most respects the blubber fatty acids of the two harbor seals (Table 2) resemble those of commercial seal oils (i.e. mostly harp seals) which are a composite sample from thousands of animals (Ackman et al. 1971a; Jangaard and Ke 1968). Though 16:1 and also total monoethylenics appeared to be somewhat lower in these two animals than in the two other individual harbor seals studied previously (Jangaard et al. 1963; Ackman et al. 1972), and high in the grey seal, the proportions 16:1 > 16:0, typical of seal oils, is still observed.

Heart triglycerides — The triglycerides, unlike the phospholipids, were present in varying proportions in tissue of the three hearts (Table 1). The total saturated acids were present in similar proportions of total triglyceride fatty acids, but with a marked replacement of 14:0 by 18:0 in the grey seal. The totals for saturated acids were lower than in the heart triglyceride of the single harbor seal analyzed earlier (31.9%), but the latter had more 16:0 (17.19%). All heart triglycerides had saturated acids totalling up to twice the percentage for the corresponding blubbers. The 16:1ω7 in the three heart triglycerides varied from 3.3 to 14.5% (previous value 7.9% for the single harbor seal) and, except in harbor seal 2, were markedly less than in the corresponding blubbers. The total percentages of 18:1 in cardiac triglycerides were approximately equal to those in the corresponding blubber in the two harbor seals (29.2 and 27.4 in animal 1; 25.4 and 26.0 in animal 2), but more dissimilar in the grey seal (26.4 and 34.0). The interchangeability of 16:1 and 18:1 led to reasonably consistent percentage totals for $\Sigma 16{:}1+\Sigma 18{:}1$ in cardiac and blubber triglycerides of harbor seals (37.3 and 39.5 in animal 1; 41.2 and 39.4 in animal 2; 45.1 and 48.8 in the animal studied by Ackman et al. 1972). The corresponding grey seal percentage totals were markedly different (respectively, 30.2 and 53.8). The total triglyceride monoethylenic acids in the three animals examined for this report showed a wide range (34.8–62.9%). Fluctuations in 16:1, 20:1, and 22:1 seemed to account for most of this. Consideration of total triglyceride 20:1 and 22:1 (including an isomer ratio to be discussed later) gives the following details:

	Harbor seal							
	1		2		Ackman et al. (1972)		Grey seal	
	Heart	Blubber	Heart	Blubber	Heart	Blubber	Heart	Blubber
Σ% 20:1	8.1	8.5	10.1	11.1	11.3	7.5	3.3	6.6
% 20:1ω9/%20:1ω11	2.0	8.1	3.9	7.8	5.2	3.5	3.8	6.7
Σ% 22:1	2.0	3.0	2.6	7.3	1.3	2.0	0.4	0.7

suggesting that the percentages of 20:1 in the heart triglyceride are variable but resemble those in the corresponding blubber. The heart triglyceride 22:1 on the other hand is approximately half that in the blubber.

Among the polyunsaturated acids the cardiac triglycerides of the grey seal are distinguished by very high levels of ω6 (or linoleic type) fatty acids. This is not a single acid effect as in addition to 18:2ω6 and the normal successor acids, 20:4ω6 and 22:5ω6, even 16:2ω6, were also affected in a detectable manner. This extreme deposition of 20:4ω6 and 18:2ω6 lowers the proportion of 22:5ω3 and of 22:6ω3 in the heart triglyceride of the grey seal, but curiously 20:5ω3 is actually increased relative to the other two animals, where 20:5ω3, 22:5ω3, and 22:6ω3 are reasonably consistent, as they are in the blubber of all three animals. The heart triglycerides of these three animals are about as unsaturated as the blubber, whereas heart triglyceride in the single harbor seal examined earlier was deficient in the C_{20} and C_{22} polyethylenic acids. For unknown reasons the heart lipid of that animal and of the pathologically abnormal seal collected for this study (data not included) were both difficult to dissolve in benzene and left a brown layer on the top of the gel column.

TABLE 1. Lipid recovery data and biological information for two harbor seals and one grey seal.

	Animal		
	Harbor 1	Harbor 2	Grey
Date collected	Feb. 7, 1973	Mar. 27, 1973	Mar. 27, 1973
Sex	Male	Female	Male
Age (*months*)	10	23	3
Weight (*kg*)	26.1	34.4	32.8
Heart weight (*g*)	250	268	290
% lipid recovered from heart	1.10	1.40	1.80
% triglycerides recovered from lipid	18.7	23.8	26.0
% phospholipids recovered from lipid	67.3	57.3	39.1
mg triglyceride/g heart	2.0	3.3	4.6
mg phospholipid/g heart[a]	7.4	8.0	7.0
Liver weight (*g*)	905	1020	900
% lipid recovered from liver	3.76	3.46	2.27

[a] 5.6 mg/g for the heart of another harbor seal (Ackman et al. 1972).

TABLE 2. Fatty acid compositions (w%) of heart, blubber, and liver lipids of two harbor seals and one grey seal.

										Liver		
	Heart triglycerides			Blubber triglyceride esters			Heart phospholipids			Phospholipids	Total fatty acids	
	Harbor seal 1	Harbor seal 2	Grey seal	Harbor seal 1	Harbor seal 2	Grey seal	Harbor seal 1	Harbor seal 2	Grey seal	Harbor seal 1	Harbor seal 2	Grey seal
12:0	0.38	0.73	ND[a]	0.17	0.20	0.14	0.01	NSA[b]	NSA	NSA	NSA	NSA
14:0	5.44	6.74	0.86	4.39	5.10	3.52	0.42	0.69	1.79	0.72	2.09	1.72
4, 8, 12 TMTD	0.09	0.11	0.05	0.21	0.05	0.13	ND	0.04	0.04	0.01	0.05	ND
Iso 15:0	0.22	0.29	0.02	0.11	0.19	0.13	0.02	0.10	0.02	0.03	0.05	0.08
Anteiso 15:0	0.11	0.07	0.02	0.05	0.10	0.04	0.01	0.06	0.01	0.01	0.02	0.05
15:0	0.36	0.40	0.19	0.38	0.38	0.29	0.54	0.20	0.27	0.24	0.39	0.43
Iso 16:0	0.07	0.07	0.08	0.09	0.07	0.08	0.05	0.06	0.09	0.06	0.05	0.11
Pristanic	ND	0.02	ND	0.02	0.02	ND	ND	ND	ND	0.04	0.05	0.12
16:0	13.36	12.87	11.84	10.47	10.38	9.16	11.40	12.44	12.65	15.44	18.48	17.76
Iso 17:0	0.39	0.07	0.63	0.03	0.14	0.07	0.28	0.34	0.76	0.17	0.30	0.15
Anteiso 17:0	0.18	0.02	0.21	0.01	0.09	0.03	0.09	0.10	0.22	0.14	0.10	0.10
17:0	0.21	0.53	0.49	0.66	0.65	0.62	0.35	0.43	0.44	0.74	0.86	0.84
Phytanic	0.24	0.02	ND	0.05	0.05	0.06	0.05	0.05	ND	0.03	0.07	0.05
Iso 18:0	0.18	0.14	0.44	0.18	0.16	0.14	0.16	0.10	0.26	0.27	0.05	0.10
18:0	3.67	1.55	14.26	1.26	1.30	0.52	14.71	11.43	14.73	21.33	16.91	16.25
19:0	0.10	0.08	0.01	0.21	0.15	0.15	0.10	0.09	0.09	0.06	0.05	0.05
20:0	ND	0.07	0.05	0.09	0.10	0.03	0.02	0.02	0.05	0.14	0.05	0.06
22:0	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Total saturated	24.9	23.8	29.1	18.4	19.1	15.1	28.2	26.1	31.4	39.4	39.6	38.7
14:1ω9	0.26	ND	0.09	0.14	0.10	0.14	ND	0.10	0.40	ND	0.03	ND
14:1ω7	0.44	1.17	0.52	1.03	0.77	0.81	0.25	1.59	1.37	0.01	0.05	0.03
14:1ω5	ND	ND	0.09	ND	ND	ND	0.05	ND	ND	ND	ND	ND
15:1	0.11	0.09	0.08	0.03	0.07	0.04	ND	0.10	0.18	0.05	0.05	0.02
16:1ω11	0.29	0.57	ND	0.32	0.56	0.26	0.06	ND	ND	0.11	0.20	Trace
16:1ω9	0.86	0.57	0.34	0.32	0.56	0.26	0.19	0.29	0.17	0.35	0.61	0.69
16:1ω7	6.99	14.51	3.35	12.06	12.15	19.06	1.41	3.08	3.13	2.37	5.08	6.28
16:1ω5	0.30	0.21	0.08	0.08	0.14	0.26	0.19	0.19	0.04	0.28	0.51	0.21
17:1ω10	ND	ND	0.02	ND	ND	ND	ND	ND	ND	ND	0.30	ND
17:1ω8	0.67	0.37	0.08	0.52	0.56	0.50	0.28	0.10	0.12	0.26	0.91	0.47
18:1ω11 (approx.)	2.40	4.00	ND	1.00	1.00	1.10	ND	0.50	ND	0.60	0.80	0.30
18:1ω9 (approx.)	21.80	15.66	18.39	20.78	18.41	24.41	15.12	13.46	17.74	13.02	13.55	11.60
18:1ω7	4.62	5.02	7.55	5.19	5.86	7.47	5.16	4.53	6.48	8.63	6.78	11.08
18:1ω5	0.35	0.70	0.49	0.41	0.73	1.03	0.09	0.15	0.17	0.68	0.40	0.21
19:1	0.17	0.17	0.02	0.18	0.18	0.14	0.32	0.05	0.05	0.11	0.20	0.23
20:1ω11	2.60	2.00	0.51	0.89	1.20	0.73	0.91	1.59	0.59	0.81	0.79	0.30
20:1ω9	5.19	7.73	1.95	7.19	9.34	4.88	2.33	3.74	1.37	1.50	2.96	1.07

20:1ω7	0.35	0.28	0.77	0.36	0.54	0.99	0.16	0.15	0.55	0.18	0.15	0.61
20:1ω5	ND	0.07	0.06	0.04	0.05	0.05	ND	0.03	0.06	0.08	0.02	ND
22:1ω11 + 13	1.87	2.19	0.20	2.44	6.51	0.43	0.68	1.11	0.17	0.13	0.73	ND
22:1ω9	0.17	0.38	0.20	0.51	0.72	0.28	0.01	0.32	0.21	0.15	0.05	ND
22:1ω7	ND	ND	ND	0.03	0.02	0.02	ND	ND	0.01	0.01	ND	ND
24:1	ND	ND	ND	ND	ND	ND	ND	ND	ND	0.21	ND	ND
Total monoethylenic	49.4	55.7	34.8	53.5	59.5	62.9	27.2	31.1	32.8	29.5	34.2	33.0
16:2ω4?	ND	ND	ND	ND	ND	ND	0.28	ND	ND	ND	0.30	ND
16:2ω6?	ND	ND	0.62	0.05	0.14	0.07	0.28	0.38	0.75	0.34	ND	ND
18:2ω9?	ND	ND	ND	0.03	0.02	ND	ND	ND	ND	0.09	0.07	0.05
18:2ω6	1.98	1.83	4.27	1.24	1.24	0.97	3.41	3.98	4.69	1.96	3.19	3.85
20:2ω9	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
20:2ω6	0.15	0.10	0.08	0.23	0.18	0.10	0.23	ND	0.09	0.13	0.10	ND
22:2ω6	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND	ND
Total diethylenic	2.1	1.9	5.0	1.6	1.0	1.1	4.2	4.3	5.5	2.5	3.7	3.9
16:3ω3	0.08	0.15	0.35	0.24	0.19	0.24	0.16	ND	0.30	0.06	0.35	0.62
18:3ω6	0.04	0.09	0.05	0.16	0.14	0.08	0.09	0.19	0.01	0.01	0.16	0.11
18:3ω3	0.76	0.65	0.21	ND	0.57	0.27	0.02	0.25	0.25	0.06	0.24	0.10
20:3ω6	ND	ND	0.20	0.04	0.07	0.02	0.09	ND	0.29	0.43	0.22	ND
20:3ω3	0.04	0.08	ND	0.10	0.08	0.06	ND	ND	0.10	ND	ND	0.12
20:3ω9	ND	ND	0.05	0.08	0.04	0.03	ND	ND	ND	0.47	0.07	ND
Total triethylenic	0.9	1.0	0.9	0.6	1.1	0.7	0.4	0.4	0.9	1.0	1.0	0.9
16:4ω1	ND	0.28	ND	0.25	0.22	0.45	ND	0.17	ND	ND	ND	ND
18:4ω3	0.75	1.14	0.05	1.11	0.89	0.69	0.04	0.05	0.02	0.01	0.11	0.06
20:4ω6	3.74	1.54	14.33	0.91	0.70	0.66	18.53	13.61	15.88	16.17	10.45	17.95
20:4ω3	0.22	0.22	0.05	0.42	0.31	0.44	0.09	ND	0.02	0.14	ND	0.15
22:4ω6	0.14	ND	ND	0.26	0.24	0.10	ND	ND	ND	0.33	0.27	ND
22:4ω3	ND	ND	0.14	0.04	0.07	0.01	ND	ND	ND	ND	ND	ND
Total tetraethylenic	4.8	3.2	14.6	3.0	2.4	2.3	18.7	13.8	15.9	16.6	10.8	18.2
20:5ω3	4.56	4.40	7.72	7.34	4.35	5.23	9.20	11.66	8.25	3.60	7.10	3.79
21:5ω3	0.09	ND	ND	0.33	0.25	0.16	ND	ND	0.18	0.04	ND	ND
22:5ω6	0.05	ND	0.28	0.11	0.07	0.02	0.10	ND	0.13	0.09	ND	ND
22:5ω3	3.37	3.18	1.03	5.18	3.95	4.94	0.67	0.47	0.75	2.39	1.08	0.49
Total pentaethylenic	8.1	7.6	9.0	13.0	8.6	10.3	10.0	12.1	9.3	6.1	8.2	4.3
22:6ω3	8.88	7.15	2.28	9.61	8.09	7.12	4.03	3.71	1.88	4.46	2.27	0.66
Unknowns (including acetals)	1.08	0.27	4.33	0.73	0.28	0.60	7.42	8.36	2.15	0.37	0.48	0.97
I.V. (calc.)	134.5	125.4	133.3	152.9	132.7	138.3	148.5	144.6	136.8	128.6	115.4	115.9

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[a] ND = not determined, usually indicating that minor amounts were not sought for technical reasons.

[b] NSA = no significant amount present (usually 0.01% or less).

Phospholipids of heart and liver — The fatty acids of the phospholipids from the three hearts may be compared with those of the phospholipids isolated from one liver, and with the fatty acids from the two total liver lipids which were shown by thin-layer chromatography to be essentially all phospholipid (less than 5% each of triglyceride and sterol ester). The percentages of total saturated acids are higher in the three liver lipids, but do not differ markedly in any particular acid. Among the monoethylenic acids the totals do not differ appreciably. There is more 16:1ω7 in the liver phospholipids than in the heart phospholipids. In the liver phospholipids of both harbor seals this results in a 2:1 ratio for the 18:1ω9 and 18:1ω7 (cis-vaccenic acid arising from chain elongation of 16:1ω7) acids as against 3:1 in heart phospholipids. In the grey seal another unexpected variation is observed. In the liver phospholipids the proportions of the "ω7" series of monoethylenic fatty acids stemming from the 16:1ω7, which is itself higher than for the two harbor seals, are sufficiently unusual that 18:1ω7 is almost equal to 18:1ω9 (oleic acid), as well as being relatively important as 20:1ω7. The liver lipids are mostly functional rather than depot in nature but could be responsible for the high proportion of 18:1ω7 to 18:1ω9 in the heart triglyceride which may be influenced by the particular isomeric acids circulated from the liver. The phospholipids of heart and the liver contained modest proportions of 20:1 (up to 5.5%) and of 22:1 (up to 1.4%). The high values occur in harbor seal 2, where heart triglyceride monoethylenic acids were also high. The blubber as well is rich in 20:1 and 22:1 in harbor seal 2. The polyunsaturated fatty acids in these polar lipids are difficult to compare in detail. An excessive level of "ω6" acids in the grey seal modified proportions of other longer-chain polyunsaturated acids. On the other hand, the interdependence of 20:4ω6 and 20:5ω3 is demonstratable also in the polar lipids of harbor seal 2 as the latter is high when the former is low (compared to harbor seal 1 and the grey seal).

Discussion — As a result of continued exposure to 22:1 and 20:1 acids in the diet, or as depot fat mobilized into the vascular system, seals apparently resemble pigs and possibly some smaller animals in accumulating these acids in cardiac triglycerides as modest percentages of total fatty acids but in proportions differing from those in blubber and hence probably as highly modified versions of dietary fatty acids. The proportional fatty acid isomer distributions suggest that individual isomers are degraded and/or accumulated in much the same way in seals as in rats.

Our results must be interpreted with caution as only three animals of two species were examined. Large feral animals also tend to show wide deviations from the "norm" of any parameter under consideration due to the effects of age, sex, general health, and state of nutrition. In the absence of any "control" animal it is not known if the high triglyceride content of the heart tissue of the 3-mo grey seal (Table 1) is comparable to the temporary lipidosis found in experimental laboratory animals. In the rat, phospholipids are a relatively constant proportion of cardiac tissue at all ages, but total lipid and triglyceride show erratic variations (see Carlson et al. 1968; Lang and Riemold 1971; Egwin and Kummerow 1972; Szuhaj 1969), making it impossible to attach significance to this one result for the grey seal. In normal humans an average total lipid in tissue of heart septa was 26.5 mg/g, of which 13.2 mg/g was phospholipid and 3.5 mg/g triglyceride (Fletcher 1972). However, age variations for cardiac total lipid, possibly reflecting triglyceride increase, were, respectively, 28.8, 35.3, 40.9, and 54.1 mg/g tissue at ages 6, 23, 39, and 46 yr (Ferrell and Radloff 1972). The two heart tissue triglyceride results for the more mature harbor seals could show a comparable steady increase in triglyceride with age, as this does not seem to be due to accumulation of 22:1 or 20:1 in the heart such as observed in long-term laboratory feeding studies with some species (see Beare-Rogers and Nera 1972; Rocquelin et al. 1973). The in-text comparisons of these two acids in heart and blubber triglycerides (see above) indicate instead that the increase of 22:1 in blubber with age reported by Jangaard and Ke (1968), which presumably reflects dietary changes in fatty acid intake (see below), is barely detectable in heart triglycerides. Earlier studies with rats provide ample evidence for deposition of dietary 22:1 throughout body tissues (reviewed by Jacquot et al. 1969; Rocquelin and Cluzan 1971; Rocquelin et al. 1971), although this may be slight in peritoneal and subcutaneous fats (Braekkan et al. 1968). The feeding of margarines, including some incorporating partially hydrogenated marine oils, to rats for 7 and 12 mo led to separate but seemingly parallel deposition relationships for 20:1 and 22:1 acids in subcutaneous or perirenal fats versus cardiac tissue (Ziemlanski et al. 1972b). The results for 20:1 are less informative but this acid is not always handled in parallel to 22:1. For example Walker (1972b) found that after 6 wk pig hearts had deposited 4.3% 20:1 and 3.3% 22:1 from a diet containing 9.4% and 27.1%, respectively, of these acids. The proportions in plasma were intermediate, suggesting modification of chain length in the liver. The liver has been demonstrated to be an active site for chain shortening of 22:1 to 18:1 (Lapous et al. 1970), although 18:1 in human plasma was not increased by ingestion of rapeseed oil (Trémolières et al. 1972).

Conacher et al. (1973) have shown that the dietary monounsaturated fatty acid isomer distribution is only slightly altered during accumulation and/or turnover in cardiac triglyceride in rat-feeding tests. Referring to the ratio (in text) of 20:1ω9/20:1ω11 for seals one finds that in cardiac tissue the ratio is only half that for blubber in the three animals of this study. If the blubber acid isomers reflect an average of dietary proportions, then 22:1ω11 (the GLC peak includes some ω13 not separable by open-tubular GLC) is actively being chain-shortened by β-oxidation to 20:1ω11 on or before deposition in the cardiac triglyceride. This effect is also reported in rats by Conacher et al. (1973) for both normal cis acids and the abnormal trans isomers. As precise quantitation of 18:1ω11 relative to 18:1ω9 is not possible by GLC technology alone, the continuation of this degradation process in the 18:1 acids (Table 2) is only an approximation. A comparative study of peak shapes confirms that 18:1ω11 is a higher proportion of total 18:1 in heart triglycerides than in blubber as shown in Table 2. On the other hand 16:1ω11 is clearly separated from other 16:1 isomers (R. G. Ackman, Department of the Environment, Fisheries and Marine Service, Halifax Laboratory, Halifax, N.S., unpublished data) and an equal accumulation of ω11 and ω9, both minor isomers, can be detected in the cardiac triglycerides and blubber (also shown in Table 2). The 20:1ω9/20:1ω11 ratios for the liver lipids for the three animals were, respectively, 1.9, 3.7, and 3.6, virtually identical with the cardiac triglyceride ratios. In the cardiac phospholipids the same ratios were, respectively, 2.6, 2.4, and 2.3, closer to the cardiac triglycerides than to the blubber triglycerides. This suggests that in these seals the β-oxidation of monoethylenic acids is not localized in cardiac tissue but may take place elsewhere and that the isomers deposited in the heart triglycerides depend upon the proportions in which fatty acids are transported from the intestinal lymph or liver to the heart.

Seal pups are born with some blubber fat and are generously supplied with milk approaching 50% fat in extreme cases (D. E. Sergeant, Department of the Environment, Fisheries and Marine Service, Arctic Biological Station, Ste. Anne de Bellevue, Quebec, personal communication; see also Ackman et al. 1971a). The milk may thin as nursing is terminated (3–4 wk) but contains up to 5% 22:1 and 15% 20:1 (Jangaard and Ke 1968), although much lower figures have been reported for the grey seal (Ackman and Burgher 1963). As 22:1 and 20:1 percentages in the fats of pups are similar to the milk levels or to those in nursing females, the nursing pups are exposed to conditions accepted as predisposing to cardiac lipidosis (see pigs, Beare-Rogers and Nera 1972).

The diets of seals vary somewhat with species and in the young harp seal certainly include invertebrates such as euphausiids (Mansfield 1967), in which these longer-chain fatty acids are in a low or moderate proportion of total fatty acids (Ackman and Eaton 1966; Ackman et al. 1970). However, all older animals eat fish of diverse species (Sergeant 1959, 1973; Spalding 1964) where the levels of docosenoic acids may be as high as 30% or as low as 15% of the total fatty acids (Ackman 1973), and thus approximate experimental conditions used for fatty acid studies with laboratory animals (e.g. Beare-Rogers et al. 1971). A typical experimental rat diet (No. 10, Beare-Rogers et al. 1972a), including 18:2ω6 at 21.3%, 18:3ω3 at 7.3%, no 20:1, and 22:1ω11 at 30.7% led to cardiac lipidosis after 1 wk and to an abnormal cardiac total lipid fatty acid composition of:

16:0	7.1%	18:1	27.8%	18:2ω6	16.2%
18:0	11.9%	20:1	2.5%	20:4ω6	9.1%
		22:1	23.0%	22:6ω3	2.5%

showing both the typical deposition of 22:1 and some chain shortening to 20:1. Deposition of long-chain fatty acids in the hearts of mice is less if feeding of the experimental diet is every 2nd day instead of every day (Staron and Moreau 1972), but harbor seals probably feed steadily on a particular fish species as long as it is readily available (Spalding 1964).

The success of seals in maintaining and multiplying populations under conditions of activity, cold, and stress (Bigg 1969; Mansfield 1967; Sergeant 1959, 1973; Spalding 1964) suggests that newborn seals should be investigated by rearing in controlled experiments to determine if these longer-chain fatty acids cause any long-term adverse effects in animals approximating man in size and with some variety in diet. Appropriate rearing conditions have been developed for harp seals (Ronald et al. 1970).

Most of the minor acids given in Table 2 for cardiac triglycerides and phospholipids which are typical of marine oils (Ackman et al. 1971a), can be found in trace amounts in many terrestrial animals but are seldom listed. The marine aspects of the seal heart triglycerides and phospholipids include the 20:5ω3 and 22:5ω3 which are minor components of rat heart lipids (see above, also Walker 1972a). Linoleic (ω6) acids are obvious in hearts of rats on vegetable oil diets, and 22:6ω3 at 1.4–6.2% possibly reflects the dietary availability to the rat of 18:3ω3 precursor. (For the effect of un-hydrogenated fish oil in the rat heart see Lang and Reimold 1971 and Teige and Beare-Rogers 1973).

The fatty acids of the 3-month-old grey seal are unusual in two respects. These are, respectively, the unusual proportions of "ω6" acids, especially 18:2ω6 and 20:4ω6 which are high, except in the blubber where they are comparatively low, and by the "ω7" family of monoethylenic fatty acids. Possibly at age 3 mo, a diet deficient in fish but including invertebrates, some of which may be rich in "ω6" acids (Ackman et al. 1970, 1971b), would account for this unusual feature (compare pigs, Walker 1972b). Most fish lipids and fats are quite low in "ω6" acids (Ackman 1973). Walker (1972a) has commented on the competition between "ω3" and "ω6" acids in the rat and this relationship may extend to the unusual proportions of 20:5ω3 and 22:6ω3 in the grey seal organ lipids (Table 2). Alternatively conservation of the "essential" ω6 acids could lead to their being removed from the blubber of grey seals during periods of fat turnover and/or depletion, with temporary storage in organ lipids. The western North Pacific subspecies (*Phoca vitulina largha*) of the harbor seal may lose nearly half their blubber (based on thickness measurements) after weaning and when they move from ice floes into a swimming life stage (Naito and Nishiwaki 1972). We have no comparable data for Nova Scotia grey seals. A diet of invertebrates low in fat could also lead to the necessity of synthesizing a proportion of monoethylenic acids to keep the important depot fat in compositional balance, starting with 16:1ω7 formed de novo from 16:0 (Ackman et al. 1971a), and also including new 18:1ω9, resulting in the percentages for all isomers of these acids in the blubber triglycerides totalling 53.8% as against 30.2% in the cardiac triglyceride. The grey seal would appear to be a more suitable subject for further investigation than the harbor seal as the communal habits of the former would facilitate collection of multiple samples covering a desirable range of ages.

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Geographical Distribution of Alleles for Supernatant Malate Dehydrogenase in Walleye (*Stizostedion vitreum vitreum*) Populations from Western Canada

J. W. Clayton, R. E. K. Harris, and D. N. Tretiak

Department of the Environment
Fisheries and Marine Service
Freshwater Institute, Winnipeg, Man. R3T 2N6

Clayton, J. W., R. E. K. Harris, and D. N. Tretiak. 1974. Geographical distribution of alleles for supernatant malate dehydrogenase in walleye (*Stizostedion vitreum vitreum*) populations from western Canada. J. Fish. Res. Board Can. 31: 342–345.

Walleye (*Stizostedion vitreum vitreum*) populations from western Canada contain three alleles for supernatant malate dehydrogenase (MDH). The protein subunits specified by these alleles produce isozymes that are readily distinguished by starch gel electrophoresis procedures. One of the MDH alleles (c^1) appears to reach a maximum frequency of about 0.6 in the walleye populations of Crean and Montreal lakes, two headwater lakes in central Saskatchewan. The frequency of this allele declines to about 0.1 in populations only a relatively short distance downstream from these headwater lakes. In most walleye populations tested the c^2 and c^3 alleles predominate at frequencies between 0.2 and 0.7, whereas c^1 is usually comparatively rare and occurs at a frequency of about 0.05.

Clayton, J. W., R. E. K. Harris, and D. N. Tretiak. 1974. Geographical distribution of alleles for supernatant malate dehydrogenase in walleye (*Stizostedion vitreum vitreum*) populations from western Canada. J. Fish. Res. Board Can. 31: 342–345.

Les populations de dorés jaunes (*Stizostedion vitreum vitreum*) de l'ouest canadien contiennent trois allèles pour la malate déshydrogénase surnageante (MDH). Les sous-unités protéiques déterminées par ces allèles produisent des isozymes que l'on peut facilement distinguer par des techniques d'électrophorèse sur gel d'amidon. Un des allèles de la MDH (c^1) semble atteindre une fréquence maximale d'environ 0.6 chez les populations des lacs Crean et Montréal, deux lacs de la tête des eaux du centre de la Saskatchewan. La fréquence de cet allèle diminue à environ 0.1 chez des populations qui se trouvent à une courte distance seulement en aval de ces lacs. Chez la plupart des populations de dorés analysées, les allèles c^2 et c^3 prédominent à des fréquences allant de 0.2 à 0.7, alors que c^1 est ordinairement relativement rare et se rencontre à une fréquence d'environ 0.05.

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The genetics of multiple electrophoretic forms of supernatant malate dehydrogenase (MDH) isozymes in walleye (*Stizostedion vitreum vitreum*) have already been described (Clayton et al. 1971). The limited data available at that time clearly indicated the existence of considerable variation in frequencies of *c* MDH alleles among a few walleye populations. Clayton et al. (1971) suggested that this range in gene frequency could be useful in the evaluation of the introduction of walleye fry into waters that contain depleted natural populations. The survey described in this note was undertaken as a preliminary step to the fry transfer experiment with the view to determining the range of variation in MDH gene frequency that could be anticipated in walleye populations from western Canada. Some data presented previously (Clayton et al. 1971, 1973) are included here to provide the most comprehensive record available at present.

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Materials and methods — In May 1972, 345 walleye were trapped from a spawning run at Crean Lake in Prince Albert National Park, Saskatchewan. These fish were anesthetized with M.S. 222 (*m*-aminobenzoic acid ethyl ester methane sulphonate, Kent Chemicals, Vancouver) and muscle samples were taken from the live fish with modified hypodermic needles as described by Uthe (1971). Some of these fish were selected as parental stock for fry to be transferred to another lake in an experiment currently in progress. An additional 72 fish were taken from this stock in 1971. The 1971

TABLE 1. Occurrence of malate dehydrogenase phenotypes and calculated gene frequencies for walleye (*Stizostedion vitreum vitreum*) populations of western Canada.

Water body		No. of fish and CC MDH phenotype[a]						Gene frequencies			99% CL for c^1 frequency
		1,1	1,2	1,3	3,3	2,3	2,2	c^1	c^2	c^3	
Churchill River system											
L. Waskesiu, Sask.	o	18	10	24	4	6	1	0.556	0.143	0.302	0.440–0.672
	e	19.4	10.0	21.1	5.7	5.4	1.3				
Crean L., Sask.	o	150	6	204	57	–	–	0.611	0.007	0.381	0.564–0.656
	e	155.9	3.7	194.5	60.6	2.3	0.02				
Montreal L., Sask.	o	16	7	17	4	–	1	0.622	0.100	0.278	0.479–0.748
	e	17.4	5.6	15.6	3.5	2.5	0.4				
Egg L., Sask.	o	5	4	16	3	8	4	0.375	0.250	0.375	0.245–0.529
	e	5.6	7.5	11.2	5.6	7.5	2.5				
Lac La Ronge, Sask.	o	2	8	3	5	23	19	0.125	0.575	0.300	0.056–0.215
	e	0.9	8.6	4.5	5.4	20.7	19.8				
Moose L., Alta.	o	–	2	1	–	7	6	0.09	0.66	0.25	0.011–0.30
	e	0.1	2.0	0.7	1.0	5.2	6.9				
Doré L., Sask.	o	3	8	4	–	11	17	0.209	0.616	0.174	0.110–0.344
	e	1.9	11.1	3.1	1.3	9.2	16.3				
Pinehouse L., Sask.	o	1	16	3	5	33	44	0.103	0.671	0.225	0.053–0.167
	e	1.1	14.1	4.7	5.2	30.9	46.0				
South Indian L., Man.	o	–	8	2	3	16	19	0.104	0.646	0.250	0.038–0.202
	e	0.5	6.5	2.5	3.0	15.5	20.0				
Nelson River system											
First Cranberry L., Man.	o	–	4	7	5	5	3	0.229	0.312	0.458	0.098–0.426
	e	1.3	3.4	5.0	5.0	6.9	2.3				
Saskatchewan R. at The Pas, Man.	o	–	2	1	4	7	1	0.10	0.37	0.53	0.12–0.32
	e	0.1	1.1	1.6	4.3	5.9	2.0				
Cedar L., Man.	o	–	2	–	4	7	7	0.05	0.57	0.38	0.0026–0.21
	e	0.05	1.1	0.7	2.8	8.6	6.1				
L. Winnipegosis, Man.	o	–	–	–	31	45	24	0.0	0.465	0.535	
	e	–	–	–	28.6	49.7	21.6				
L. Winnipeg, Man.	o	–	8	2	9	45	22	0.058	0.564	0.378	0.0222–0.122
	e	0.3	5.6	3.8	12.3	36.6	27.3				
Sasaginnigak L. Man.	o	–	–	1	2	6	4	0.04	0.54	0.42	0.0002–0.25
	e	0.02	0.5	0.4	2.3	5.9	3.8				
Red R. at Lockport, Man.	o	–	–	1	10	20	16	0.011	0.553	0.436	0.00005–0.072
	e	0.005	0.5	0.4	8.9	22.7	14.4				
L. of the Woods, Ont.	o	2	11	5	40	118	116	0.034	0.618	0.348	0.016–0.052
	e	0.3	12.4	6.9	35.3	125.5	111.6				
Waters of English River system, Ont.	o	–	16	9	17	69	119	0.054	0.702	0.243	0.028–0.081
	e	0.7	17.5	6.1	13.6	78.6	113.4				
Mackenzie River system											
L. Athabasca, Alta.–Sask.	o	–	2	11	17	7	3	0.162	0.187	0.650	0.073–0.294
	e	1.0	2.4	8.4	16.9	9.7	1.4				

[a] o, e: observed and expected (calculated) phenotype distributions.

fish were killed prior to taking the muscle samples. Fish from Pinehouse, Doré, Egg, Montreal, Athabasca, and South Indian lakes, as well as from Lac La Ronge, were obtained from commercial sources. The samples from Moose, Cedar, and Sasaginnigak lakes, as well as from the Saskatchewan River, were accumulated at the Freshwater Institute as part of a heavy metal contamination survey. Some of the Lake Winnipeg samples were also obtained in this way. Clayton et al. (1973) have already described a similar source of walleye samples from Lake of the Woods and the English River system in northwestern Ontario. The present fish from Waskesiu Lake, Lake Winnipegosis, and some of the Lake Winnipeg samples are specimens described previously (Clayton et al. 1971).

The technique of starch gel electrophoresis, the sources of various chemical reagents, and the identification of walleye supernatant malate dehydrogenase (MDH) phenotypes and genotypes have all been described (Clayton et al. 1971). Confidence limits for gene frequency were derived from a table by Mainland et al. (1956).

Results and discussion — Table 1 shows the distribution of supernatant MDH phenotypes in many walleye populations from western Canada, the calculated gene frequencies for these populations, as well as the calculated (Castle-Hardy-Weinberg) distribution of phenotypes. In most cases there is reasonable agreement between the observed and "expected" distribution of phenotypes. Calculations were not extended to include an evaluation of the probability of the fit between the observed and expected phenotype distributions for two reasons. In many samples the expected numbers in some classes are very small and the x^2 statistic is not directly applicable. Other samples such as the fish from the English River system and fish from some of the large lakes are unlikely to represent a single interbreeding population. In this case there is no true "expected" distribution and further calculations become meaningless. We include a calculated gene frequency for each sample to show the range to be expected and to provide a common basis for comparing the various populations. Differences in the frequency of the c^1 allele seem to be the most important interpopulation variable and we include in Table 1 the 99% confidence limits for the c^1 allele frequency for each sample to aid in assessing the significance of this variable.

The frequency of the c^1 allele exceeds 0.5 in only three populations from Lake Waskesiu, Crean Lake, and Montreal Lake (Table 1). The unique genetic composition of these populations is de-

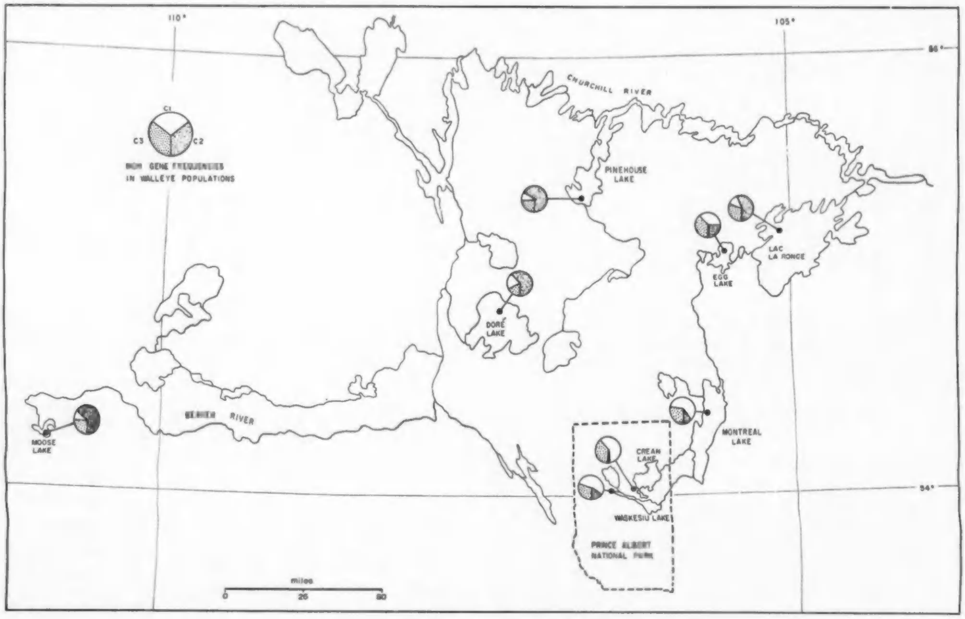

FIG. 1. Map showing gene frequencies for malate dehydrogenase alleles in walleye (*Stizostedion vitreum vitreum*) populations from waters within and near Prince Albert National Park, Saskatchewan.

monstrated by the fact that no other population was found to have a c^1 allele frequency within the 99% confidence limits for any of these three populations. The drainage connections among the lakes with these unique walleye populations are shown in Fig. 1 together with graphical representations of the walleye MDH allele frequencies. A steep cline in the frequency of the c^1 allele in populations along the Montreal River is evident in Fig. 1. The Lake Waskesiu, Crean Lake, and Montreal Lake walleye populations also have an unusually low frequency of the c^2 allele in comparison with all the other populations sampled (Table 1).

Outside the map area of Fig. 1, only two walleye populations from First Cranberry Lake, Manitoba, and Lake Athabasca on the Alberta–Saskatchewan boundary, show c^1 allele frequencies significantly greater than 0.1 (Table 1). In southern Manitoba and northwestern Ontario the c^1 allele is rare and its frequency is considerably lower than 0.1 (Table 1).

If only the populations from central Saskatchewan are considered (Fig. 1), the distribution of the c^1 allele could be considered to be consistent with the occurrence of c^1 as a new mutation with some adaptive advantage in a walleye population in the vicinity of Montreal Lake. The present distribution of allele frequencies could have arisen as a result of natural selection for the c^1 allele in or near Montreal Lake together with migration of fish carrying the c^1 allele. Alternatively, it is possible that the c^1 mutation has occurred several times and is somehow of selective advantage in certain locations. This latter hypothesis might more reasonably account for the moderate frequency of c^1 in populations from such distant locations as Lake Athabasca and First Cranberry Lake (Table 1). In these widely separated populations the possibility that protein subunits like c^1 with discontinuous geographic distribution could be produced by more than one allele should also be considered. This question can be decided only after intensive investigation of the structure of the MDH subunits. In a parallel study of lactate dehydrogenase in frogs, similar reservations were expressed and in one case electrophoretically identical isozymes from widely separated populations were shown to differ in a sensitive immunological test (Salthe 1969). These limitations of our knowledge regarding the real nature of the MDH alleles do not limit the practical value of the MDH phenotypes as a biological "tag" in this species that is highly valued in both the commercial and recreational fisheries.

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Renal Tubular Morphology in the Channel Catfish (*Ictalurus punctatus*) Kidney

M. W. KENDALL[1] AND D. E. HINTON[2]

Department of Anatomy, School of Medicine
and
Water Resources Laboratory, University of Louisville, Louisville, Ky.

KENDALL, M. W., AND D. E. HINTON. 1974. Renal tubular morphology in the channel catfish (*Ictalurus punctatus*) kidney. J. Fish. Res. Board Can. 31: 346–347.

Kidneys of 50 channel catfish (*Ictalurus punctatus*) (25–30 cm long) obtained from a fish hatchery were subjected to light microscopic examination. All renal tubular segments generally found in freshwater teleost kidney were present. These included a ciliated neck segment, bisegmental proximal segment, ciliated intermediate segment, distal segment, and, in addition, collecting ducts.

KENDALL, M. W., AND D. E. HINTON. 1974. Renal tubular morphology in the channel catfish (*Ictalurus punctatus*) kidney. J. Fish. Res. Board Can. 31: 346–347.

Nous avons examiné au microscope optique le rein de 50 barbues de rivière (*Ictalurus punctatus*) (25–30 cm de longueur) provenant d'un établissement de pisciculture. Tous les segments tubulaires du rein généralement rencontrés dans le rein des téléostéens d'eau douce sont présents. Ils comprennent un segment de col cilié, un segment proximal bisegmenté, un segment intermédiaire cilié, un segment distal et, en plus, des canaux collecteurs.

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ASSESSMENT of the effects of environmental pollutants on fish has often been delayed by a lack of histological literature concerning various fish organs (Hinton et al. 1972). The renal tubular morphology of many fish species is not known. Since the teleost kidney is readily damaged by various agents (Trump and Bulger 1967; Kendall 1972) it is necessary to describe its structure to establish a standard of normalcy to which pathologic-induced alterations may be compared. The channel catfish (*Ictalurus punctatus*) frequently occurs throughout Canada and the USA and because of its abundance and wide distribution it is an excellent research specimen for toxicological and water quality tests (Hinton et al. 1973). This study describes the renal tubular morphology of the channel catfish as a model for future toxicological experimentation. This description then may be used for comparative purposes to characterize adequately the specific renal tubular lesions in channel catfish.

Materials and methods — Fifty channel catfish, 25–30 cm long, were obtained from a fish hatchery near Shelbyville in Shelby County, Kentucky. The fish were stunned and kidneys removed immediately.

Kidneys for routine histological examination were placed in Regaud's or Bouin's fixative, transferred to 70% alcohol for storage, and subsequently dehydrated in alcohol, cleared in xylene, and embedded in paraffin. Serial sections were cut at 6 μ on a rotary microtome. The staining methods employed included H and E (hematoxylin and eosin), PTAH (phosphotungstic acid hematoxylin), PAS+H (periodic acid-Schiff's reagent plus hematoxylin), and Pollak's polychrome using methods of McManus and Mowry (1960).

Observations — The catfish kidney has no zones of cortex and medulla as in mammals. Rather, it consists of coiled tubules arranged in no specific pattern (Fig. 1 and 2).

The glomerulus is a tuft of capillaries with afferent and efferent arterioles (Fig. 1 and 2), respectively. Interstitial hemopoietic tissue forms an abundant parenchyma between tubules and glomeruli. The initial portion of the renal tubule is referred to as the neck segment (Fig. 1). In the neck segment where numerous cilia occur, the squamous cells of the glomerular capsule blend immediately with the cuboidal cells lining the neck segment (Fig. 1). Distally, a sharp transition occurs to the next segment, designated here as the first proximal

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[1] Present address: Department of Anatomy, University of Mississippi, School of Medicine, Jackson, Miss.

[2] Present address: Department of Pathology, University of Maryland, School of Medicine, Baltimore, Md.

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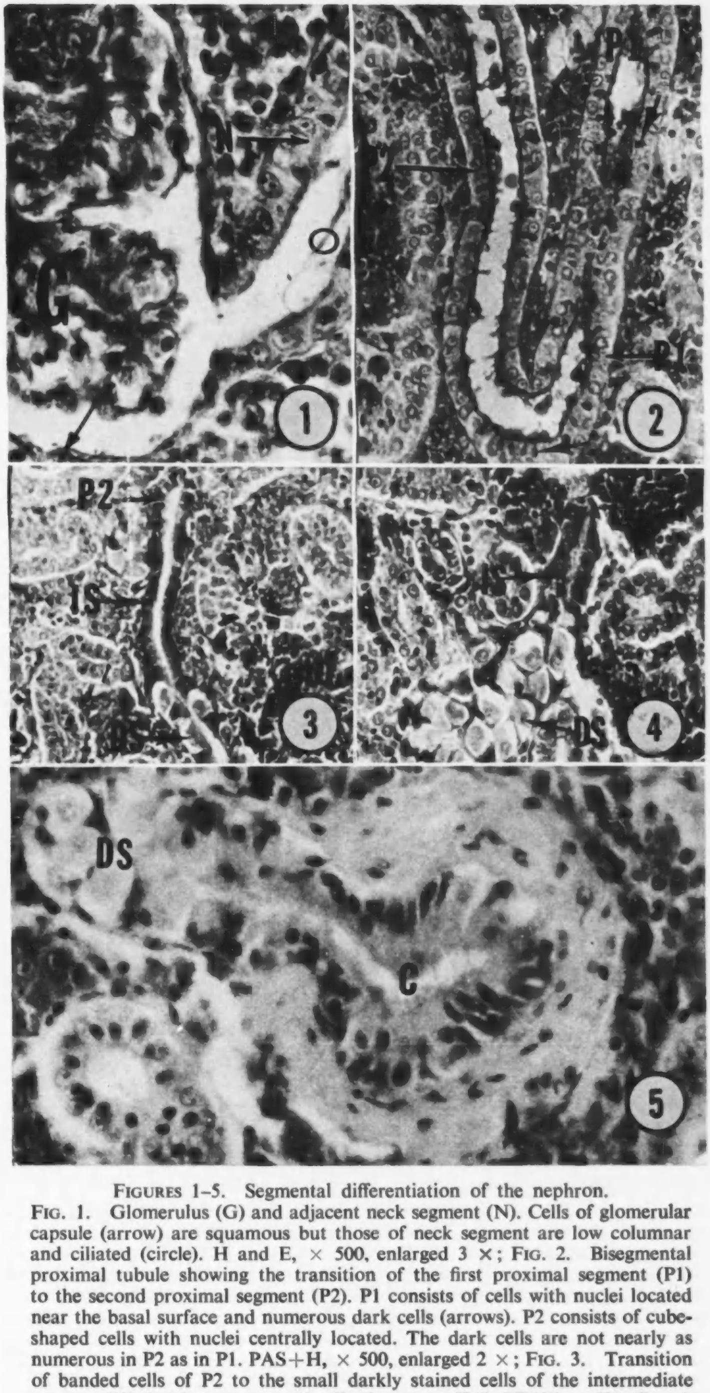

FIGURES 1–5. Segmental differentiation of the nephron.
FIG. 1. Glomerulus (G) and adjacent neck segment (N). Cells of glomerular capsule (arrow) are squamous but those of neck segment are low columnar and ciliated (circle). H and E, × 500, enlarged 3 ×; FIG. 2. Bisegmental proximal tubule showing the transition of the first proximal segment (P1) to the second proximal segment (P2). P1 consists of cells with nuclei located near the basal surface and numerous dark cells (arrows). P2 consists of cube-shaped cells with nuclei centrally located. The dark cells are not nearly as numerous in P2 as in P1. PAS+H, × 500, enlarged 2 ×; FIG. 3. Transition of banded cells of P2 to the small darkly stained cells of the intermediate segment (IS) that in turn enters the distal segment (DS). PTAH, × 500; FIG. 4. Transition of IS to DS. Note that the cells of the distal segment are roundish with a prominent centrally placed nucleus. PTAH, × 500, enlarged 1⅓ ×; Fig. 5. The transition of distal segment (DS) to the collecting duct (C). Cells of the collecting duct are pseudostratified columnar epithelium and surrounded by a thick sheath of smooth muscle and connective tissue. Pollak's polychrome, × 500, enlarged 2 ×.

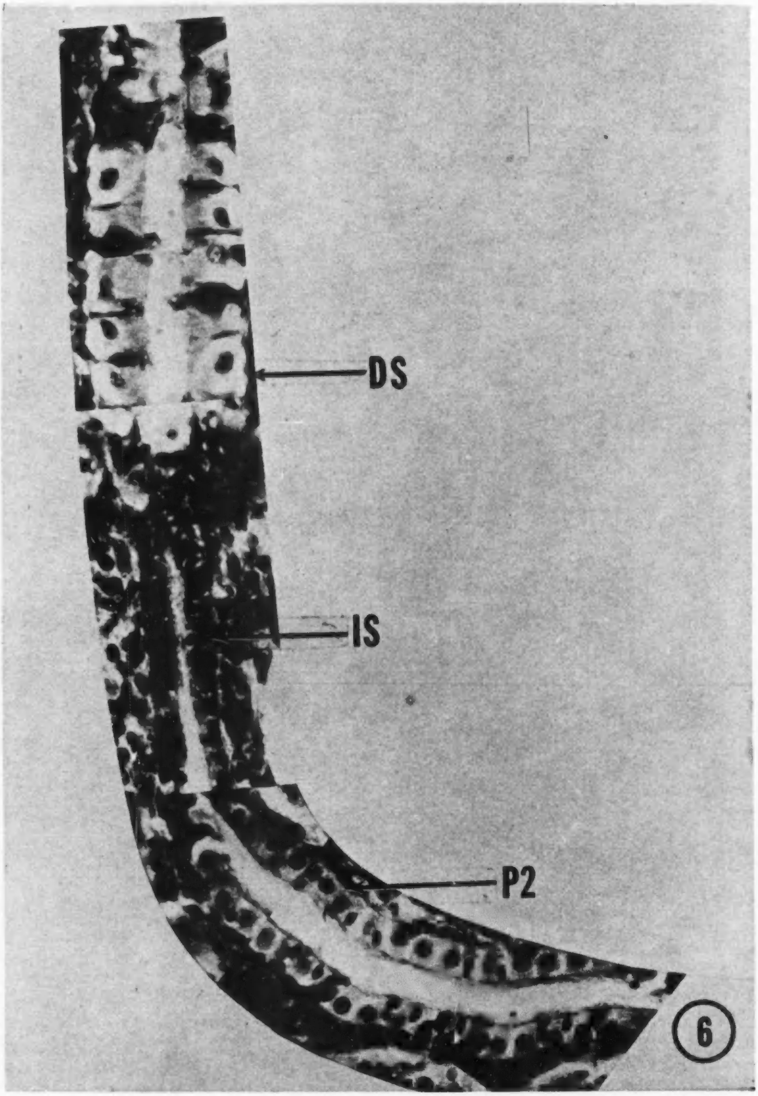

FIG. 6. Partial reconstruction of nephron. The transition zones between segments are clearly shown. This was accomplished by fitting together photographs from six contiguous serial sections eight thick. The transition from the second proximal segment (P2) to the ciliated intermediate segment (IS) is sharply demarcated. The intermediate segment (IS) is quite constricted as compared to the wide distal segment (DS). Pollak's polychrome stain, × 1000, enlarged 1.8 ×.

segment (P1). This first proximal segment (Fig. 2) is characterized by low columnar epithelium with a prominent periodic acid-Schiff (PAS) positive brush border. In addition, numerous dark nuclei of small cells (Fig. 2) are located near the luminal surface of this epithelium. As one proceeds distally along the tubule gradual reduction in height of proximal tubular epithelium is noted, with eventual transition to the second proximal segment (P2) (Fig. 2 and 3). This portion of the renal tubule is characterized by cuboidal epithelium with brush border and a few dark nuclei. The nuclei of lining epithelial cells are located centrally. Cytoplasm near cell borders usually stains less intensely than than that nearer the nucleus, thus giving the tubule a banded appearance.

The photographic reconstruction (Fig. 6) shows the sharp transition of cuboidal epithelium of the second proximal tubule (P2) to the narrow ciliated intermediate segment (Fig. 3 and 4). The intermediate segment (IS) is narrower than either the second proximal segment or the ensuing distal segment (DS), and consists of closely packed cells that are darkly stained (Fig. 3, 4, and 5). Near the distal end of the intermediate segment are found wavy cilia (Fig. 4 and 6). The intermediate segment is difficult to find in all serial sections and may be absent from some tubules. Generally, however, its lack of appearance in H and E preparations is due to the fact that H and E staining techniques do not adequately differentiate this segment. Tubular epithelium of the distal segment (Fig. 3, 4, and 6) consists of thickened cell borders. The distal segment (DS) is shown (Fig. 5) entering the collecting duct (C). Pseudostratified columnar epithelium lines the collecting tubule and remains unchanged in its course to the ureter. A thick layer of smooth muscle and connective tissue surrounds the collecting duct.

Discussion — In channel catfish we observed five segments of the renal tubule described by Edwards (1935). In addition, we observed an elaborate system of collecting ducts not comparable cytologically to similar segments in higher vertebrates.

With special histological staining techniques (Pollak's polychrome and PTAH) we have shown that a ciliated intermediate segment is present in channel catfish. This differs from Grafflin's (1937) contention that its presence was questionable.

Our observations are also consistent with those of Hickman and Trump (1969) who demonstrate proximal and distal segments in kidneys of yellow bullhead (*Ictalurus natalis*) but did not fully describe all the available segments.

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We also thank Prof J. B. Longley for helpful guidance.

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Marking Atlantic Salmon (*Salmo salar*) with Oxytetracycline

P. H. ODENSE AND V. H. LOGAN

Department of the Environment
Fisheries and Marine Service, Halifax Laboratory, Halifax, N.S.

ODENSE, P. H., AND V. H. LOGAN. 1974. Marking Atlantic salmon (*Salmo salar*) with oxytetracycline. J. Fish. Res. Board Can. 31: 348–350.

The marking of Atlantic salmon (*Salmo salar*) by feeding oxytetracycline has been investigated. Fluorescent marks, readily visible for up to 2 yr postfeeding have been observed in centrum and rib with the former being superior for gross observation. Best results were obtained with fish more than 1 yr old. Sampling, storage, and observation techniques are discussed.

ODENSE, P. H., AND V. H. LOGAN. 1974. Marking Atlantic salmon (*Salmo salar*) with oxytetracycline. J. Fish. Res. Board Can. 31: 348–350.

Nous avons étudié la possibilité de marquer des saumons atlantiques (*Salmo salar*) en les nourrissant d'oxytétracycline. Des marques fluorescentes, facilement visibles jusqu'à 2 ans après ingestion, ont été observées dans le centrum et les côtes, les premières étant supérieures pour examen microscopique. Les meilleurs résultats ont été obtenus avec des poissons âgés de plus d'un an. Nous discutons de l'échantillonnage, de l'entreposage et des techniques d'observation.

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THE use of tetracycline antibiotics in marking various fish species has been studied by several groups (Weber and Ridgway 1962, 1967; Kobayashi et al. 1964; Jensen and Cumming 1967; Scidmore and Olson 1969; Yamada 1971; and Trojnar 1973). These compounds become chelated in developing bone and form a yellow-gold fluorophor visible under ultraviolet light (360 mn). They are easily administered in the food and are presently used in some Canadian fish hatcheries for prophylaxis and treatment of disease.

Weber and Ridgway (1967) found the fluorescent mark was stable in Pacific salmon (*Oncorhynchus* spp) and rainbow trout (*Salmo gairdneri*) for 3½ yr with no effect upon the fishes' survival rate. A certain amount of interspecific variation appears to exist, since these workers found a good mark was produced in ribs and centrum of coho salmon whereas Scidmore and Olsen (1969) found these tissues marked poorly in walleye. However, these differences may also have been produced by differences in tetracycline administration techniques. Four groups of Atlantic salmon were therefore treated or examined to determine the effectiveness of this type of tagging on this species.

Methods — Group A — Two-year-old smolts were fed Veterinary grade Terramycin at a level of 250 mg oxytetracycline hydrochloride/kg fish per day. The antibiotic was fed in 2% agar cubes containing 3.5% liver infusion broth and 0.3% glucosamine to aid tetracycline absorption (Gittinger and Wiener 1960). Initially, the average weight of the fish was 20 g. They were fed the cubes for 5 days and then 60 days later were fed for another 10 days. They were examined (i) 7 days after the first feeding, (ii) 25 days after the second feeding, and (iii) 11 mo after the second feeding at which time their average weight was 127 g. Fish frozen for over 12 mo after the first two samplings were reexamined (iv).

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Group B — One and a half-year-old parr from a federal fish culture station were sampled 11 mo after being fed oxytetracycline hydrochloride for 2 wk at a level of 1.3% w/w in their diet. The daily consumption per fish was unknown. Their mean weight was 26 g when sampled.

Group C — Two and a half-year-old postsmolts from a commercial fish culture station were sampled 4 mo after being fed 660 mg Terramycin/kg fish per day for 9 days. Their mean weight was 408.6 g when sampled.

Group D — Three and a half-year-old grilse, both hatchery and wild from the River Phillip, Nova Scotia spawning run were examined. The hatchery fish had been fed 1.3% w/w oxytetracycline hydrochloride in their diet 23 mo prior to sampling. Their mean weight was 3200 g when sampled.

The bones to be examined were removed, boiled in water, scraped, and air dried (Weber and Ridgway 1962). The tissue must be scraped from the surface of the centrum or the fluorophor will be masked. The bones were examined using an 8 W long-wave ultraviolet hand lamp as a light source. The fish were examined externally and internally, noting especially the following specific structures: teeth, gill rakers, ribs, centra, skull, and otoliths. Where gross observations were augmented with microscopic observations, a 250-W mercury source lamp was used with UG-1 and BG-12 exciter filters, a BG-38 infrared absorbing filter, and a Leitz 470 ultraviolet supression eyepiece filter.

TABLE 1. Localization of the deposited tetracycline fluorophor in various structures of the Atlantic salmon (*Salmo salar*).

Group	No.	External	Teeth	Gill raker	Rib	Centrum	Skull	Otolith
A 2-year-old								
(i) 7 days postfeed	3	+[a]	+	+	+	+	?	?
(ii) 25 days postfeed	3	+[a]	+	+	+	+	?	?
(iii) 11 mo postfeed	5	–	–	–	+	+	–	–
(iv) i and ii storage 1 yr	6	–	+	+	+	+	–	?
B 1½-year-old	6	–	–	–	–	–	–	–
C 2½-year-old	20	–	–	+	+	+	+	–
D hatchery	4	–	–	–	+	+	–	–
wild	8	–	–	–	–	–	–	–

[a]External fluorescence was occasionally visible in the mandible, maxillary, operculum orbital, and fin ray; + = readily visible, – = not readily visible, ? = not examined.

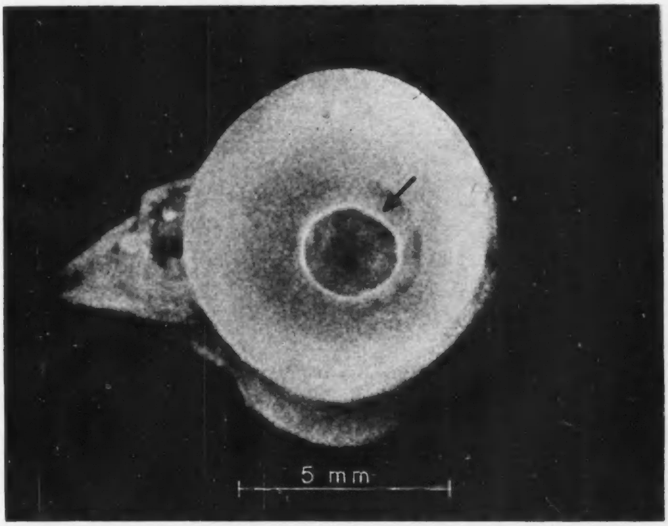

FIG. 1. Vertebra from a 3½-year-old clipped Atlantic salmon (*Salmo salar*) grilse as seen under long-wave ultraviolet illumination. Note the bright fluorescent ring in the centrum (arrow).

Results and discussion — The results are given in Table 1. The best fluorophor, visible as a bright yellow ring (Fig. 1) was present in the centrum. The ribs also fluoresced, although the fluorophor was usually limited to only a thin line in the proximal $\frac{1}{3}$ of the rib in the case of older fish. External fluorescence and that in the teeth, skull, and gill rakers were visible initially but faded after a period of time and were not readily visible in the older specimens. The otolith was not visibly fluorescent.

Weber and Ridgway (1967) noted that negative results may result from exposure to light, absorption of bone, or deposition of bone over the fluorophor. Sectioning or grinding may reveal the latter but would be impractical for large scale studies.

The negative results obtained with the parr may be better explained on the basis of a size factor. Weber and Ridgway (1967) reported variations in marking quality with size of fish and the Atlantic salmon parr examined may have been beneath the "threshold" for good marking when they were fed the previous year, when they would have been smaller than group A fish.

It is not necessary to remove the bone from the fish. The caudal peduncle can be bisected and as long as a full view of a centrum is presented, the tissue can be scraped off the bone examined in situ. However, if the bone is to be removed for later examination it must be stored in a dark place to avoid the photolytic effect of light.

When the bone is examined in situ one must be well aware of the possible presence of normal yellow fluorescent material such as fat which may lead to confusion. The bare bone surface must be exposed.

We feel that feeding Atlantic salmon more than 1 year old a diet containing oxytetracycline at a level of 250 mg/kg per day or more for at least 5 days can provide a stable mark which is readily visible in the centrum when the cleaned bone is examined under long-wave ultraviolet light. Present results indicate that the marks remain for 23 mo and on the basis of experiments with other species there is every reason to expect the marks to be detectable for much longer periods.

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Effects of Cold Shock on Vulnerability of Juvenile Channel Catfish (*Ictalurus punctatus*) and Largemouth Bass (*Micropterus salmoides*) to Predation

C. C. Coutant, H. M. Ducharme Jr.,[1] and J. R. Fisher[1]

Environmental Sciences Division
Oak Ridge National Laboratory, Oak Ridge, Tenn. 37830, USA

Coutant, C. C., H. M. Ducharme Jr., and J. R. Fisher. 1974. Effects of cold shock on vulnerability of juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) to predation. J. Fish. Res. Board Can. 31: 351–354.

Acute cold stress caused increased predation on juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) by unstressed adult largemouth bass when temperature differentials were 9 and 7 C or more, respectively, (base temperatures 16 and 17 C). Predation rate tended to increase exponentially with increasing temperature differential. Catfish held 1 h in the cold water were only slightly less susceptible to predation than were others tested immediately after the temperature change.

Coutant, C. C., H. M. Ducharme Jr., and J. R. Fisher. 1974. Effects of cold shock on vulnerability of juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) to predation. J. Fish. Res. Board Can. 31: 351–354.

Un stress aigu par le froid entraîne une prédation accrue sur les jeunes barbues de rivière (*Ictalurus punctatus*) et achigans à grande bouche (*Micropterus salmoides*) par des achigans adultes non soumis à un tel stress, lorsque les différences de température sont de 9 et 7 C ou plus, respectivement (par rapport à des températures de base de 16 et 17 C). Le taux de prédation augmente exponentiellement avec l'augmentation de la différence de température. Les barbues maintenues pendant 1 h dans l'eau froide ne sont que légèrement moins vulnérables à la prédation que les autres qui sont soumises aux essais immédiatement après le changement de température.

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In this study, we sought to determine if sublethal abrupt decreases in temperature would measurably increase the susceptibility of juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) to predation by adult largemouth bass. Mortalities have been reported from cold shocks to fish living in, and metabolically acclimated to, warm discharge waters of thermal electric power stations (Michigan Water Resources Commission unpublished data; Pennsylvania Fish Commission unpublished data; Williams et al. 1971; U.S. Atomic Energy Commission 1972). Deaths have occurred when the heat source was suddenly terminated, when the thermal plume was rapidly dispersed by winds or currents, or when temperature at the plant intake dropped rapidly. Natural temperature drops, such as in the Great Lakes in summer when winds shift the epilimnion and cause upwelling of cold hypolimnetic water, have caused cold kills (Emery 1970).

To adequately regulate power plant shutdown to protect aquatic life, the tolerable thermal decreases must be known, not only for direct death, but for sublethal stresses that may markedly decrease long-term survival. The experiments reported here simulate field conditions where juvenile fishes that have resided in a warmed area long enough to become acclimated to the high temperatures disperse into the surrounding waters when the heated discharge terminates. The small fishes then encounter predators that have not themselves experienced the temperature drop. Both largemouth bass and channel catfish are warmwater fishes that are known to be attracted to warm discharges when ambient water is cool (e.g. Trembley 1965). We did not study the equally valid question of simultaneous cold shock of predators and prey.

Materials and methods — These experiments tested the relative survival of cold-shocked and unshocked prey when groups of the two were offered simultaneously to adult largemouth bass and about half of the combined number were allowed to be eaten. The protocol was modified from that reported by Bams (1967) and Coutant (1973). Juvenile fish from a com-

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[1] Undergraduate research participant.

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mon stock were randomly separated into groups, differentially marked, and held for more than 1 wk in 90-liter aquaria: one for each of several warm temperatures (Table 1) and others for control (unshocked) fish held at the same temperature as the predators. The fish were marked with a liquid nitrogen cold-branding technique (Coutant 1972), test fish on one side and control fish on the other. To provide simultaneous addition of test and control fish to the predator tank (17 C for bass, 16 C for catfish), groups of 15 catfish and 20 bass from an acclimation temperature and the predation temperature were combined in a 9-liter plastic pail at the predation temperature. In some tests, the acclimated fish were held at the predation temperature for 1 h prior to mixing with control fish (to test for possible recovery from the initial cold shock or progressive debilitation by cold). In tests without a holding period, the contents of the pail (fish and water) were added within 15 s to the predator tank.

Predation took place in 1.2-m-diam cylindrical fiberglass tanks with water depths of 65 cm. There were no structures other than inlet pipe, center outflow standpipe, and tank walls and bottom to provide protection for the prey. There were three or four predators per tank.

TABLE 1. Mean survival proportions for juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) acclimated to various temperatures and preyed on by adult largemouth bass at 16 and 17 C, respectively.

Acclimation Temp (*C*)	Survival proportion	
	Test	Control[a]
Channel catfish, no holding		
16	0.60(4)[b]	0.60
20	0.70(2)	0.56
22	0.67(2)	0.73
25	0.40(3)	0.82[c]
30	0.33(3)	0.87[c]
34	0.09(3)	0.96[c]
Channel catfish, 1-h holding		
22	0.65(3)	0.47
25	0.30(2)	0.70[c]
30	0.40(3)	0.80[c]
34	0.20(3)	0.89[c]
Largemouth bass, no holding		
17	0.48(3)	0.55
20	0.65(3)	0.52
24	0.44(4)	0.61[c]
30	0.05(3)	0.75[c]

[a] A fish held at predation temperature.

[b] Numbers of replicates; 15 catfish and 20 bass per replicate.

[c] Difference from equal numbers of survivors significant at $P < 0.05$.

After introduction of the prey, predators were allowed a maximum of 0.5 h to eat approximately 50% of the prey fish, at which point survivors were removed and test and control fish were counted. Length and weight determinations were made on channel catfish to determine if size was an important factor in the results. Predation for more than 0.5 h was undesirable since recovery from the initial shock or progressive debilitation by cold would be unaccounted for. Surviving prey were not used in subsequent tests. Surviving catfish were held at the control temperature for 1 mo or longer to observe any direct mortality of the test fish.

The statistic used to express the difference in predation rates on the two groups of fish is the ratio $d_p = i_1/i_2$ (Bams 1967), where i_1 and i_2 are, respectively, the instantaneous mortality rates of the test and control groups. The instantaneous mortality rate when time is a unit interval is given by $i = -\log_e s$, where s = survival proportion (i.e. number at finish divided by number at start). Group d_p was calculated for replicates by summing the numbers s. The chi-square analysis was used to test for homogeneity among replicate trials and for significance of observed differences in predation.

Both juvenile largemouth bass and channel catfish were obtained from the U.S. Fish and Wildlife Service, Frankfort National Fish Laboratory, Frankfort, Kentucky. They were maintained for several weeks in our laboratory to recover from stresses of transportation. At time of testing, bass averaged 47.8 ± 5.07 (SD) mm and 1.13 ± 0.41 g, and catfish averaged 75.0 ± 7.90 mm and 3.05 ± 0.64 g. Predator bass, 500–1300 g, were captured by electrofishing from nearby Clinch River (Watts Bar Reservoir) and were maintained in laboratory tanks for several months prior to the tests.

Temperatures in all tanks were maintained within ±0.2 C of desired temperatures (Table 1) with temperature controllers attached to 1000-W quartz rod heaters. A flow of about 0.5 liter/min passed through each tank continuously. Artificial lighting was maintained in a 12-h photoperiod.

Results — Channel catfish and largemouth bass fed to predators immediately after a temperature decrease were preyed upon in greater numbers ($P < 0.05$) than controls when the decrease was 9 and 7 C, or more, respectively, (Table 1). Channel catfish held for 1 h at the predation temperature before predation were less susceptible than those immediately exposed, although they were still preyed upon in significantly greater numbers after a 9 C temperature decrease.

The ratios of instantaneous predation rates tended to increase above 1 when the temperature change

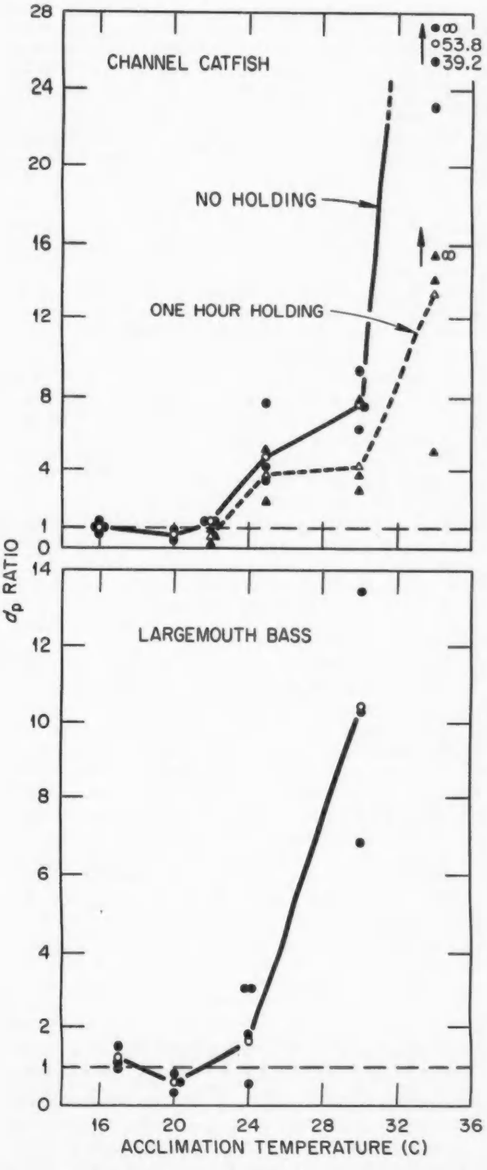

FIG. 1. Ratios of experimental instantaneous predation rates (d_p) for juvenile channel catfish (*Ictalurus punctatus*) and largemouth bass (*Micropterus salmoides*) acclimated to various temperatures and preyed on by adult largemouth bass at 16 and 17 C, respectively. Both species were preyed on immediately after instantaneous transfer from the acclimation temperature to the predation temperature, and catfish also after 1-h holding at 16 C. Solid characters represent individual tests; open characters, combined replicates. A d_p ratio of 1 indicates identical susceptibilities of cold-shocked and unshocked (control) fish to predation.

exceeded about 6 C (Fig. 1). Thereafter the increase tended to be exponential. There was also a consistent tendency ($P > 0.05$) for d_p ratios to be less than 1 after the test fish received temperature decreases less than about 6 C.

Surviving catfish from both test and control groups were similar in length to the stock fish (74.8 ± 0.64, 75.3 ± 0.64, and 75.0 ± 0.79, respectively). There was no statistical difference ($P > 0.05$).

Catfish that survived predation were held for several weeks at 16 C without direct mortality. Those which had been acclimated to 34 C, however, showed behavioral signs of stress (e.g. sluggishness, erratic swimming) that lasted for at least 24 h.

Discussion — These experimental results have shown statistically, or exhibited trends that strongly suggest, a progression of cold stress effects on young channel catfish and largemouth bass with increasing temperature differential. Most clearly, there is a debilitation of catfish and bass at differentials of 9 and 7 C or more, respectively, that decreases their ability to survive predation.

The trends indicate that tolerance may be surpassed when the differential is in the vicinity of 6 C (for base temperatures of 16 or 17 C). Although statistical significance of differences at $P = 0.05$ were not attained until larger differentials than this were reached, there is no assurance that ecological significance corresponds with the 0.05 probability level. Further experimentation, particularly with additional replicates, would be necessary to establish the exact differential that would first give statistical significance. Much more research, involving discrete field populations of catfish and bass, would be required for accurate estimation of ecologically significant levels of predation.

The pattern of response to increasing stress from temperature change in these experiments (i.e. a possible enhancement of survival relative to controls by small changes and a rapidly increasing relative susceptibility to predation with progressively larger differentials) is similar in form to responses shown to heat stress (Coutant 1973). The similarity may derive from similar behavioral and physiological manifestations of stress that affect the sequence of events leading to prey capture. The effects of temperature decrease seemed to range from stimulation by contact with the cold water to depression of the fish into a cold coma as was seen by Brett (1956). After small temperature decreases, all fish swam vigorously in the predation tank. After larger temperature decreases, shocked fish rested on the bottom in an apparently "benumbed" state, whereas control fish avoided predators and sought refuge at the perimeter of the tank's surface. In heat shock, there was also a period of reduced responsiveness even before the fish obviously lost equilibrium (Coutant 1973). Recovery from cold coma must be gradual, because tests after 1 h showed only slightly reduced effects compared with those for immediate predation.

Similarity in responses to cold stress by channel catfish and largemouth bass in these experiments corresponds well with other similarities reported in the literature. The two species are warmwater fishes with similar optimum temperatures for growth (Strawn 1961, 1970) and similar lethal temperatures (Hart 1952; Allen and Strawn 1967).

The minimum decrease in temperature that clearly increased predation on catfish in these experiments (9 C) is considerably less than the temperature decrease necessary for direct death. This was shown when fish acclimated to 34 C were placed in 16 C water without mortalities (although behavioral signs of stress lasted several hours). Hart (1952) showed that channel catfish adults could be cooled from as high as 25 C to 0 C without 50% mortality.

The most critical time for abrupt thermal decreases at power plants that would kill fish would likely be in winter when the base temperature would be near 0 C rather than in the 16–17 C range studied here. The importance of selective predation on stressed juveniles could be less then, however, because many young would have attained larger size. Large predators could also be less active in the winter months. The base temperatures used here may reasonably approximate those conditions in summer and fall when increased predation on juveniles of certain species could be an important power plant impact. The losses would go unnoticed in pollution control inspections since no carcasses would remain to identify the incidents.

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Food of Shorthorn Sculpin, *Myoxocephalus scorpius*, in the Cumberland Sound Area of Baffin Island

I. A. MOORE[1] AND J. W. MOORE[1]

Department of Industry and Development
Government of the Northwest Territories, Yellowknife, N.W.T., Canada.

MOORE, I. A., AND J. W. MOORE. 1974. Food of shorthorn sculpin, *Myoxocephalus scorpius*, in the Cumberland Sound area of Baffin Island. J. Fish. Res. Board Can. 31: 355–359.

One hundred shorthorn sculpins, *Myoxocephalus scorpius*, over 15 cm in length captured from June to October, 1972, in Cumberland Sound, Baffin Island, fed almost exclusively (90% by both numbers and dry weight) on the planktonic amphipods *Pseudalibrotus glacialis* and *Parathemisto libellula*. In contrast, 140 fish captured about the same times from nearby Pangnirtung Fjord fed heavily on the benthic gastropods *Littorina saxatilis* and *Margarites umbilicalis* (each 34% by numbers and 22% by weight) and the bivalve *Modiolaria discors* (16% by both). Drifting ice on Cumberland Sound probably reduced the level of illumination making the detection of benthic prey difficult and causing the sculpins in this area to feed entirely on the better illuminated, brightly colored plankton. At both localities, the most abundant species in the plankton and the epifauna were also the most frequently encountered in gut contents. On the other hand, coelenterates, planktonic gastropods, copepods, and infauna, all of which were abundant in the environment, were rarely eaten.

MOORE, I. A., AND J. W. MOORE. 1974. Food of shorthorn sculpin, *Myoxocephalus scorpius*, in the Cumberland Sound area of Baffin Island. J. Fish. Res. Board Can. 31: 355–359.

Cent chaboisseaux à épines courtes, *Myoxocephalus scorpius*, de plus de 15 cm de longueur, capturés de juin à octobre 1972 dans le détroit de Cumberland, île de Baffin, se nourrissaient presque exclusivement (90% en nombre aussi bien qu'en poids) des amphipodes planctoniques *Pseudalibrotus glacialis* et *Parathemisto libellula*. Par contraste, les 140 poissons capturés en même temps dans le fjord avoisinant de Pangnirtung se nourrissaient abondamment des gastéropodes benthiques *Littorina saxatilis* et *Margarites umbilicalis*, et du bivalve *Modiolaria discors*. Les deux premières espèces constituaient chacune 34% en nombre et 22% en poids des contenus stomacaux, alors que les valeurs correspondantes pour la dernière espèce étaient toutes deux de 16%. Une couche de glaces dérivantes dans le détroit de Cumberland réduisait probablement le niveau d'éclairage et rendait difficile la détection des proies benthiques, forçant ainsi les chaboisseaux de cette région à se nourrir exclusivement de plancton coloré et mieux éclairé. Aux deux endroits, les espèces les plus abondantes du plancton étaient également celles le plus communément rencontrées dans les contenus stomacaux, une relation également observée pour les espèces épifauniques. Par ailleurs, les coelentérés, gastéropodes planctoniques, copépodes et endofaune, tous abondants dans le milieu, étaient rarement consommés.

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THE food of adults of the shorthorn sculpin (*Myoxocephalus scorpius*) in southern areas of the northern hemisphere consists, in general, of amphipods, euphausids, decapods, and fish such as herring, gobies, and small cod (Wheeler 1969; Leim and Scott 1966) but there is only a small amount of published information on the feeding of arctic stocks (e.g. Macpherson 1971). In this investigation, the stomach contents of 240 sculpins longer than 15 cm captured at monthly intervals from June to October, 1972, from Cumberland Sound and Pangnirtung Fjord, Baffin Island, were identified and counted for comparison with simultaneous collections of zooplankton and benthos.

Materials and methods — The sculpins were captured during the first 3 days of each month by gillnetting (stretched mesh: 1.5–5.5 cm) at 66°08′N 66°09′W in Cumberland Sound and at 66°09′N 65°43′W in

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[1] Present address: School of Biological Sciences, University of Bath, Bath, Somerset, England.

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Pangnirtung Fjord (Fig. 1). The sampling was conducted at low tide between 1200 and 1700 h at a depth of 1–3 m (10–30 m from shore). Usually, 20 fish were taken each month from Cumberland Sound and 30 from Pangnirtung Fjord. Immediately after capture the sculpins were frozen at –40 C. In the laboratory the stomachs were removed and their contents sorted to species and enumerated. Ingested molluscs were plucked but all other organisms were left intact; all contents were dried at 105 C to constant weight. The taxonomic works of Brunel (1960), Macpherson (1971), Sars (1902, 1966), and Stephenson (1923) were used in identification.

Zooplankton were sampled between 1200 and 1500 h near low tide in the immediate vicinity of the sculpin collection areas with a nonclosing plankton-net 40 cm in diameter at the mouth with 110 meshes/cm^2. Forty hauls were made at the beginning of each month from bottom (1–3 m); through the clearness of the water, it was observed that the larger organisms (longer than 0.5 cm in length) did not avoid the net. Epifauna were removed by hand from the surface of the substrate in the same collection areas. This sampling was done at low tide between 1200 and 1700 h. Infauna were collected at the same sites and times as epifauna. A 15 × 15 cm Eckman dredge was used to sample completely a transect measuring 10 × 0.15 m.

During the study, water temperatures in the study areas never exceeded 4 C and macrophytes remained scarce. Turbidity of the water stayed below 3 joule thermal units and bottom deposits consisted of a mixture of sand and gravel with widely dispersed boulders 1–2 m in diameter. The sampling site in Pangnirtung was ice-free during most of the investigation but that in Cumberland Sound was often covered with drifting ice.

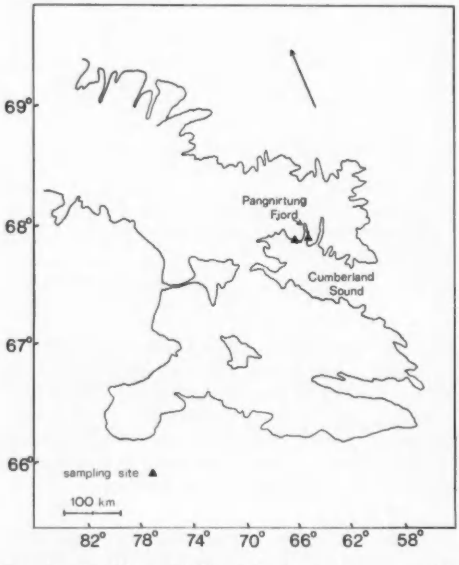

FIG. 1. Southern Baffin Island showing sampling points.

The length–weight relationship of the sculpins caught in the different samples was expressed as logarithmic regressions but significant differences ($P < 0.01$) among the slopes and positions of the lines were not found when an analysis of covariance was applied (Snedecor 1956). Thus all the data were pooled yielding the equation $\mathrm{Log}\ W = -6.4326 + 6.1107\ \mathrm{Log}\ L$ ($r = 0.79$) that indicated 15.0-cm sculpins weighed approximately 5.7 g whereas those 30.0 cm long weighed 390 g. The length distribution of the total catch showed a predominance of individuals 22.5–27.5 cm in length and the sex ratio was 1.5♂: 1.0♀.

Results and discussion — Shorthorn sculpins greater than 15 cm in length captured from Cumberland Sound fed entirely on plankton, particularly the amphipods *Parathemisto libellula* and *Pseudalibrotus glacialis*, regardless of month (Table 1). The former species accounted, on the average, for 62.2% by numbers and 50.0% by dry weight of the total stomach contents and the latter for 29.2 and 39.8%. At least six kinds of organisms were frequently encountered in the simultaneous collections of zooplankton, *Parathemisto libellula* and *Pseudalibrotus glacialis* being most common (42.1 and 29.2% by numbers, respectively); they were followed by the coelenterate *Aglantha digitale* (8.3%), and the mollusc *Clione* sp. (7.1%). *Littorina saxatilis*, although absent from the stomach contents, was overwhelmingly predominant in the epifauna (88.9% by numbers), a pattern also exhibited by several species of unidentified polychaetes in the infauna.

In Pangnirtung Fjord, on the other hand, the food consisted mainly of the benthic gastropods *Littorina saxatilis* and *Margarites umbilicalis*, the bivalve *Modiolaria discors*, and the amphipod *Pseudalibrotus glacialis*. Each of the former two species usually accounted for approximately 34% by numbers and 22% by weight of the stomach contents and *Modiolaria discors* for 16% by both numbers and weight. *Pseudalibrotus glacialis* was by far the most frequently ingested form of plankton (86% by numbers) but represented only 13% by weight of the total stomach contents. Seven species of organisms were frequently encountered in the samples of zooplankton collected with the fish. The predominant animal was always *Pseudalibrotus glacialis*, representing, on the average, 56.9% by numbers of the total haul, and followed by *Parathemisto libellula* (13.3%), the coelenterate *Bougainvillia* sp. (8.5%), and the amphipod *Gammarus ? wilkitzki* (6.2%). All five organisms collected from the epifauna belonged to the Mollusca, *Littorina saxatilis* being by far most common

TABLE 1. Mean percentages of total numbers (± SE) of organisms in the plankton and epifauna and infauna at two sites near Baffin Island on basis of monthly samples from June to October, 1972, and percentages of total number and dry weight of organisms found in the stomachs of adult shorthorn sculpins (total 240) caught during the same period.

Organism	In environment (% numbers)	In stomach contents (% numbers)	In stomach contents (% dry weight)
Cumberland Sound			
Plankton (total 1.5 animals/m³; range 0.7–2.1)			
Aglantha digitale	8.3±1.7	0.0	0.0
Bougainvillia sp.	1.6±0.2	0.0	0.0
Hybocodon sp.	1.6±0.2	0.0	0.0
Sarsia princeps	2.4±0.2	0.0	0.0
Clione sp.	7.1±0.9	0.0	0.0
Calanus hyperboreus	2.5±0.3	2.7±0.2	0.6±0.1
Mysis oculata + *M. litoralis*	1.1±0.1	3.1±0.2	1.8±0.1
Parathemisto libellula	42.1±4.7	62.2±7.2	50.0±4.9
Pseudalibrotus glacialis	29.2±1.9	29.2±3.1	39.8±4.0
P. littoralis	2.5±0.4	1.4±0.1	7.7±0.5
All other species	1.6	1.4	0.1
Total	100.0	100.0	100.0
Epifauna (75/m²; 35–125)			
Acmaea testudinalis	3.7±0.3	0.0	0.0
Buccinum cyaneum	1.6±0.1	0.0	0.0
B. sericatum	3.9±0.2	0.0	0.0
Littorina saxatilis	88.9±1.1	0.0	0.0
Margarites umbilicalis	1.9±0.1	0.0	0.0
Total	100.0	0.0	0.0
Infauna (1.5/m²)			
Unidentified polychaetes	100.0	0.0	0.0
Total	100.0	0.0	0.0
Average dry weight of stomach contents per fish: 0.4 g ± 0.19g			
Pangnirtung Fjord			
Plankton (1.6/m³; 0.8–1.9)			
Aglantha digitale	2.8±0.6	0.0	0.0
Bougainvillia sp.	8.5±2.0	0.0	0.0
Calanus hyperboreus	4.8±1.7	1.4±0.1	0.3±0.0
Gammarus ? wilkitzki	6.2±1.2	1.7±0.1	2.9±0.3
Parathemisto libellula	13.3±1.9	10.0±1.7	8.1±1.9
Pseudalibrotus glacialis	56.9±3.2	85.6±9.2	12.8±2.3
P. littoralis	1.2±0.3	0.3±0.0	1.4±0.2
All other species	6.3	1.0	0.7
Total	100.0	100.0	26.2
Epifauna (87/m²; 25–141)			
Littorina saxatilis	91.5±0.9	36.0±4.5	21.2±2.0
Margarites helicinus	0.5±0.1	4.0±1.1	1.7±0.2
M. umbilicalis	1.1±0.2	32.0±2.3	22.8±1.1
Modiolaria discors	3.1±0.4	16.0±1.6	16.2±1.8
Modiolaria faba	1.9±0.1	6.0±0.4	6.9±1.0
All other species	1.9	6.0	5.0
Total	100.0	100.0	73.8
Infauna (1.5/m²)			
Unidentified polychaetes	100.0	0.0	0.0
Total	100.0	0.0	0.0
Average dry weight of stomach contents per fish: 0.35 g ± 0.10 g			

(91.5% by numbers). Although several species of burrowing polychaetes were found in the samples of infauna, none were identified.

On the basis of the above data, shorthorn sculpins in Pangnirtung Fjord show a definite preference for feeding from the plankton in terms of numbers although benthos formed by far the largest segment of the stomach contents by weight. The most common animal encountered in the samples of plankton, *Pseudalibrotus glacialis*, was also the most frequently ingested. However, copepods were rarely eaten, a pattern which can probably be attributed to size selection (Crossman and Larkin 1959; Moore and Moore 1974). Coelenterates were also not ingested but this feature seems to be widespread among teleosts (e.g. Tyler 1972). The lack of polychaetes in the stomach contents probably reflects the difficulty involved in removing these items from the substrate, a problem apparently encountered by most other species of bottom-dwelling fishes (Keast and Webb 1966; McComish 1967; Scidmore and Woods 1960). The much more frequent occurrence of the molluscs *Margarites umbilicalis*, *Modiolaria faba*, and *M. discors* in the stomach contents than in epifaunal samples probably indicates that the fish were occasionally feeding in deeper water where these items are more abundant and where *L. saxatilis* is absent (Macpherson 1971).

The relative importance of epifauna in the diet of sculpins captured in Pangnirtung Fjord and their complete absence from the fish caught in Cumberland Sound are particularly remarkable in view of the general similarity in abundance of the animals in the two areas. An important difference between the two sites, however, is that the sound was often covered with drifting ice. It is possible therefore, that this caused a sharp drop in the level of illumination that severely restricted the visual capacity of the fish and thus made the search for food near bottom difficult. This would imply that sculpins rely heavily on vision to detect the presence of prey, a point supported by the fact that they can be easily attracted by shiny pieces of metal. Presumably, planktonic animals are better illuminated than benthos; in addition, they are often brightly colored (yellow-orange in *Pseudalibrotus glacialis* and pink in *Parathemisto libellula*), contrasting with the camouflaging of the benthos. Though other factors, such as competition for food, can force fish to change their characteristic hunting areas (Nilsson 1961, 1965), prey was so abundant in this particular case that it seems unlikely that such a factor would be of importance. Similarly, the physico-chemical environments, known to be instrumental in determining the area from which food is obtained in certain instances (Moore 1972; Warner and Fenderson 1962), were virtually alike.

Apart from sculpins, the only other species of fish commonly encountered in the study area was Arctic char (*Salvelinus alpinus*). Their food at the two sites consisted almost entirely of plankton, particularly *Parathemisto libellula* and *Pseudalibrotus glacialis* (Moore and Moore 1974). Although there was thus considerable overlap in the food of the two fish species, food was in such abundance that it seems highly unlikely that the two fishes were competing for this particular component of the environment.

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Relation Between Reproductive Potential and Sustained Yield of Fisheries

Rögnvaldur Hannesson

Department of Economics
University of Lund, Sweden.

Hannesson, R. 1974. Relation between reproductive potential and sustained yield of fisheries. J. Fish. Res. Board Can. 31: 359–362.

The steady-state yield curve is derived from the growth curve of biomass and shown to bend back toward the origin only if the relative growth rate of biomass is not a monotonically decreasing function of biomass. The bearing of this shape of the yield curve on the possibility of extinction of species is discussed.

Hannesson, R. 1974. Relation between reproductive potential and sustained yield of fisheries. J. Fish. Res. Board Can. 31: 359–362.

L'auteur dérive la courbe de rendement pour un état stable à partir de la courbe de croissance de la biomasse. Cette courbe ne se replie que si le taux de croissance de la biomasse n'est pas une fonction monotoniquement décroissante de la biomasse. La discussion porte sur l'influence d'une telle fonction rendement sur la possibilité d'extinction de l'espèce.

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In a recent article, Southey (1972) derives a steady-state yield curve that bends back toward the origin, and discusses the concurrent possibility of multiple equilibria. This note is meant to clarify how the shape of the steady-state yield curve and thereby long-term industry equilibria depend critically on the capacity of the species involved to reproduce itself.

The growth function is specified as follows:

$$\dot{W} = a(W)\cdot W \qquad (1)$$

where W is the weight of biomass, and $a(W)$ is the relative growth rate, itself a function of biomass. Two possible growth curves are shown in the NW quadrants of Fig. 1 and 2. In Fig. 1 it has the shape usually assumed, with $\delta a/\delta W < 0$ for all W, whereas in Fig. 2 this holds true only for $W > W.^*$ It is of critical importance whether or not $W^* = 0$. $W^* > 0$ means that low levels of biomass are somehow detrimental to the reproductive capacity of the population, or may, as in Fig. 2, render it unviable.

Under steady-state conditions, the yield per unit of time (Y) is equal to the rate of change of biomass:

$$Y = \dot{W}. \qquad (2)$$

The production function of the industry may be written:

$$Y = b(f,W)\cdot f\cdot W, \qquad (3)$$

where f is fishing effort. The term $b(f,W)$ expresses the catch per unit of effort as a fraction of the biomass to which it is applied:

$$Y/f = b(f,W)\cdot W, \qquad (4)$$

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and may be regarded generally as a function of fishing effort and the level of biomass.

Equations (1)–(3) define a locus

$$H(W,f) = a(W) - b(f,W)\cdot f = 0 \qquad (5)$$

determining all the combinations of biomass and effort levels that are compatible with steady-state. By the rule of implicit differentiation we know that

$$\frac{dW}{df} = -\frac{\delta H/\delta f}{\delta H/\delta W}.$$

Taking these derivatives yields:

$$\frac{dW}{df} = \frac{b(f,W) + (\delta b/\delta f)\cdot f}{\delta a/\delta W - (\delta b/\delta W)\cdot f}. \qquad (6)$$

The exact relation between b, f, and W is an empirical question and of major importance in a dynamic analysis, involving the distribution of fleets in time and space and the redistribution of the population, as part of it is removed by the fishing gear. The familiar mass-encounter hypothesis postulates a uniformly distributed population; a unit of fishing effort will in absence of congestion always remove a constant proportion of it, and consequently b is a constant and independent of effort and biomass. This is a reasonable hypothesis with regard to marine fisheries, especially when considering alternative steady-states, as it is then sufficient to assume a constant relative distribution of fish and effort for this hypothesis to hold (Beverton and Holt 1957). A number of empirical investigations that have been carried out on the basis of this hypothesis seem to give satisfactory results, including some recent studies on the North Atlantic cod fisheries (Clayden 1972).

I shall proceed by first assuming that the mass-encounter hypothesis holds. Toward the end of the article I will argue that relaxing this assumption will not thwart the conclusions arrived at on the basis of the mass-encounter hypothesis. Equation (6) then simplifies to

$$\frac{dW}{df} = \frac{b}{\delta a/\delta W}. \qquad (6')$$

Since $b > 0$, the sign of (6′) is determined by the term $\delta a/\delta W$. It follows that (6′) will always be negative when $a(W)$ is a monotonically decreasing function of W, whereas if $a(W)$ is an increasing function of W as in Fig. 2 for $W < W^*$, then (6′) will be positive in that interval. The locus $H(W,f)$ is shown in the NE quadrants of Fig. 1 and 2.

The SE quadrants are simply transformations of axis. It is now a straightforward exercise to trace the levels of yield and effort compatible with steady-state conditions. This is done in the SW quadrants. The shape of the growth curve is of critical importance for the shape of the yield curve. When the relative growth rate $[a(W)]$ is an increasing function of W as in Fig. 2, the yield curve bends back toward the origin.

Assuming the price of fish to be constant makes it possible to interpret the yield curve directly in monetary units, implicitly setting the price equal

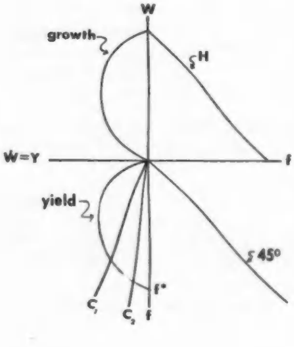

FIG. 1

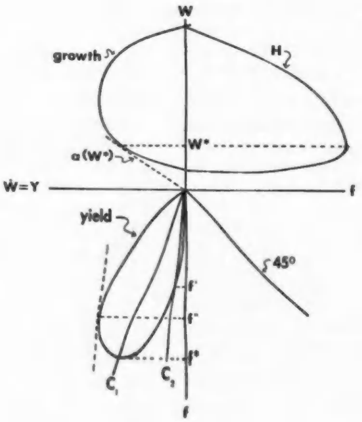

FIG. 2

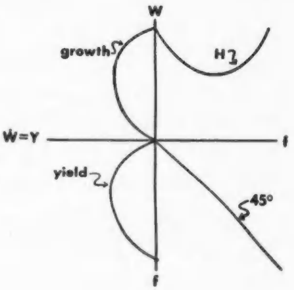

FIG. 3

to 1. Constant cost per unit of effort means that the cost curve is a straight line from the origin. Allowing for the possibility of a downward-sloping demand curve makes the geometry more complicated and may cause multiple equilibria. This has been analyzed by Anderson (1973), and I have nothing to add. It would also be possible to account for cases when cost per unit of effort is a function of effort, but the essential conclusions would not be affected by relaxing the simplifying assumption of a constant price and cost per unit of effort.

Maximizing the economic yield means selecting the level of effort where the distance between the yield curve and the cost line is maximal, as this distance represents the total net revenue.[1] Bionomic equilibrium, when fishing banks are common property and entry is free, occurs where the cost line intersects the yield curve. It follows that exploitation under common property and free entry always results in excessive fishing effort as the situation is in Fig. 1. Such is and has been the case in many fisheries characterized by common property and free entry; examples are the Pacific halibut fishery and the North Atlantic cod fishery. Also according to Fig. 1, "low" cost per unit of effort would be expected to result in large fleets and small catches per unit of effort.

Figure 2 suggests that common property may involve inefficiency of a different kind. For some cost levels (e.g. line C_1), it is still true that bionomic equilibrium implies effort in excess of that needed for maximum economic yield. But if the cost per unit of effort is lower, as C_2 represents, equilibrium effort is less than what corresponds to maximum economic yield. Given the cost line C_2, maximum economic yield may be obtained with the effort f'', whereas equilibrium effort is f'. The bionomic equilibrium nevertheless implies an inefficient industry, because the total catch is much smaller than it need be with effort at f'. If this bionomic equilibrium has been attained, the fishery has become stuck in a "low catch trap," resulting from a low and unproductive level of biomass, where a low mortality and thereby small effort is sufficient to remove all the surplus production the stock is capable of yielding. Consider the steady-state condition (2), which may be written, using (3)

$$\frac{\dot{W}}{W} = b(f,W)\cdot f.$$

On the left we have the growth per unit of time, expressed as a fraction of biomass, and on the right we have the production per unit of time, also expressed as a fraction of biomass (see Eq. 4). If the relative growth rate falls as W decreases, fishing effort must be reduced (for b constant) if a new equilibrium is to be obtained. This is what happens for "unproductive" levels of biomass; i.e. $W < W^*$ as $\delta a/\delta W > 0$ in Fig. 2. Thus one may expect "low" cost and catches per unit of effort together with a small fleet in single species fisheries, where the growth function of the biomass is of the kind shown in Fig. 2.

It is one thing to describe the characteristics of a possible "low catch trap," and another to establish that any fishing industry will ever find itself in such a situation. In fact, things are likely to be much worse than suggested by the trap, if the yield curve bends back toward the origin. Instead of getting caught in the trap, the basis of the fishery is likely to be destroyed altogether by extinction of the species. By the aid of a rudimentary dynamic analysis it is possible to show that the danger of extinction is a good deal greater for populations that are characterized by a yield curve as in Fig. 2 than for populations in Fig. 1. Consider a once and for all fall in cost per unit of effort (the same result obtains by analogy for a rise in price). The cost line falls from C_1 to C_2 in Fig. 1 and 2, and the bionomic equilibrium effort will be increased in Fig. 1, but decreased in Fig. 2; yet in both cases the competitive fishery will respond to the increase in net revenue by expanding effort. The initial response of the fishing industry will imply an approach towards equilibrium in Fig. 1, but a further deviation from equilibrium in Fig. 2. As effort is expanded the stock will be reduced and the catch per unit of effort depressed, acting as a brake on the expansion of effort. It is easy to imagine that this mechanism ensures that the new equilibrium will be attained in Fig. 1, although the industry may "overshoot the target." In Fig. 2 it is not sufficient to halt the expansion of effort, but necessary to turn it into the reverse, as the adjustment to the new equilibrium requires a contraction and not an expansion of effort. This would happen when the level of biomass and the catch per unit of effort fell far enough. A new equilibrium would occur only when effort had fallen to the extent that catch would equal the growth of the new, smaller population.

This comparison between the necessary adjustment processes in the two figures may be of aid in understanding the extinction of certain animals. The difference between the two fisheries depicted in Fig. 1 and 2 is not the possibility but the probability of extinction as a result of fishing. Extinction occurs in Fig. 1 if effort exceeds f^* and stays long enough for the stock to vanish. This could happen with an unfortunate combination of a high rate of entry and a low rate of exit in the industry, but there is no incentive for an immediate expansion of effort beyond f^* unless the cost per unit of effort falls below zero. Extinction also occurs in Fig. 2 if effort is expanded beyond f^* and maintained long enough, but it will occur too, if effort is expanded from an equilibrium in that part of the yield curve that bends back toward the origin, provided it is not contracted quickly enough to a level lower than which it started. There is an incentive for an immediate expansion of effort to a level that is incompatible with the continued existence of the species, even at a cost per unit of effort that is greater than zero (in Fig. 2 if C falls from a level equal to or lower than C_1). A population characterized by a growth curve such as in Fig. 2 faces a greater risk of extinction than the population in Fig. 1.

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[1] This is true only when there is no discounting, but discounting would not affect the conclusions.

One would not expect the type of situation described in Fig. 2 to occur in marine fisheries, because of the immense reproductive capacity of fish.[2] Inability of small populations to form schools, which may reduce predation, might bring this about (Brook and Riffenburgh 1960; Clark 1974).

Allowing for the possibility that b is a function of f does not change the conclusion that a growth curve of the kind shown in Fig. 1 ($\delta a/\delta W < 0$ for all W) will not give rise to a yield curve that bends back to the origin. Equation (6) then becomes

$$\frac{dW}{df} = \frac{b(f) + (\delta b/\delta f)\cdot f}{\delta a/\delta W}. \qquad (6'')$$

If the yield curve is to bend back to the origin, it is necessary that the slope of locus H, i.e. Eq. (6″), be negative for W in the neighborhood of virgin state equilibrium, approach infinity as W decreases, and then change sign as W is reduced below some critical level. This can only happen if $\delta a/\delta W \rightarrow 0$ and changes sign as W decreases, which does not happen in Fig. 1. The sign of (6″) may possibly become positive as f increases. It is not unreasonable to suppose that $\delta b/\delta f > 0$ for "low" and $\delta b/\delta f < 0$ for "high" levels of effort. The vessels in a small fleet may aid one another in finding fish, for example, whereas a large fleet may involve congestion. This may give rise to a locus that looks like H in Fig. 3. Congestion rather than a depleted population may be the cause of a dome-shaped steady-state yield curve, but it ought not to be difficult to distinguish between the two in empirical work.

Relaxing the assumption that b is independent of W, we end up with Eq. (6). If its denominator is to approach zero, it is necessary that $\delta b/\delta W < 0$, as long as $\delta a/\delta W < 0$. This might happen as a result of gear saturation, that is not likely to occur for a technologically efficient fleet. It would also happen if the distribution of the population became less dispersed as a result of decreasing its number, which does not seem likely either. It seems highly improbable that anything except a relative growth rate that is an increasing function of biomass in some interval will give rise to a steady-state yield curve that bends back toward the origin.

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[2] If the stock-recruitment relation is characterized by "recruitment depensation," it means that $W^* > 0$, and the yield curve bends back to the origin (Clark 1974).

Length-Weight Relations of Pacific Ocean Perch (*Sebastes alutus*) in the North Pacific Ocean

S. J. WESTRHEIM

Department of the Environment
Fisheries and Marine Service
Pacific Biological Station, Nanaimo, B.C.

AND V. A. SNYTKO[1]

WESTRHEIM, S. J., AND V. A. SNYTKO. 1974. Length–weight relations of Pacific ocean perch (*Sebastes alutus*) in the North Pacific Ocean. J. Fish. Res. Board Can. 31: 363–366.

Length–weight relations for Pacific ocean perch (*Sebastes alutus*) were determined by the iterative method from data collected aboard Soviet research vessels in the North Pacific Ocean, from Kamchatka, USSR (53°N lat), to Oregon, USA (44°N lat). Interarea values of a (in $W = aL^b$) ranged from 0.0076028 (females, E Bering Sea) to 0.054000 (females, W Bering Sea); and b, from 2.6345 (females, W Bering Sea) to 3.1694 (females, E Bering Sea). Empirical tests indicated that individual area formulae generally produced acceptable calculated weights. Interarea comparisons of calculated weights provided additional evidence of the existence of discrete stocks and two subspecies of Pacific ocean perch in the North Pacific Ocean.

WESTRHEIM, S. J., AND V. A. SNYTKO. 1974. Length–weight relations of Pacific ocean perch (*Sebastes alutus*) in the North Pacific Ocean. J. Fish. Res. Board Can. 31: 363–366.

Nous avons établi des relations longueur-poids de perches de mer du Pacifique (*Sebastes alutus*) par la méthode itérative, à partir de données recueillies à bord des navires de recherches soviétiques dans le Pacifique Nord, depuis le Kamchatka, URSS (53° lat N), jusqu'à l'Orégon, E.U. (44° lat N). Les valeurs de a (dans $W = aL^b$), d'une région à l'autre, s'étalent de 0.0076028 (femelles, mer de Béring E) à 0.054000 (femelles, mer de Béring O); celles de b, de 2.6345 (femelles, mer de Béring O) à 3.1694 (femelles, mer de Bering E). Des tests empiriques démontrent que les formules appliquées à des régions individuelles donnent des poids calculés généralement acceptables. Les comparaisons interrégionales des poids calculés fournissent une preuve de plus de l'existence de stocks discontinus et de deux sous-espèces de *S. alutus* dans le Pacifique Nord.

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DURING the first two Canada–USSR Scientific Meetings on Fisheries, in 1971 and 1972, scientific data dealing with fish stocks of mutual interest were exchanged. Among these data were length-weight measurements of Pacific ocean perch (*Sebastes alutus*) caught by Soviet research vessels in the North Pacific Ocean.

These data were compiled, processed, and compared with similar data published elsewhere.

Materials and methods — All fish were caught by trawl. Length, sex, and weight data were collected at sea. Each fish was measured to the nearest 0.1 cm, fork length, and weighed to the nearest 10 g. Most samples were random, and consisted of 50 or 100 fish.

Samples were grouped arbitrarily into the following nine areas, which generally conform with subdivisions suggested by Barsukov (1964) and/or Westrheim (1970).

Area	Approximate extent
W Bering Sea (west of 180° long)	53–62°N
E Bering Sea (east of 172°W)	61°N
Aleutian Islands	165 E–170°W
Unimak	166–164°W
Kodiak	153–148°W
Yakutat	147–137°W
SE Alaska	56°14′–54°34′N
British Columbia	51°38′–48°49′N
Washington–Oregon	47°55′–44°44′N

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[1] Present address: Pacific Scientific Research Institute of Fisheries and Oceanography, Vladivostok, USSR.

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TABLE 1. Length–weight coefficients[a] for Pacific ocean perch (*Sebastes alutus*) by area, 1966–71.

Area	Year	Males			Females		
		N[b]	*a*	*b*	N[b]	*a*	*b*
W Bering	1966; 1969–71	580 (25–46)	0.029923	2.7762	592 (27–46)	0.054000	2.6345
E Bering	1970–71	545 (22–44)	0.025601	2.8088	371 (20–47)	0.0076028	3.1694
Aleutian	1966; 1969–71	767 (19–42)	0.041569	2.6621	695 (19–46)	0.044816	2.6511
Unimak	1968; 1970–71	320 (20–40)	0.016641	2.9290	220 (21–39)	0.022552	2.8409
Kodiak	1971	153 (23–40)	0.014168	2.9881	144 (22–40)	0.012263	3.0303
Yakutat	1971	204 (24–40)	0.015672	2.9692	146 (26–41)	0.012265	3.0376
SE Alaska	1971	178 (22–40)	0.020336	2.8854	217 (22–42)	0.018239	2.9240
British Columbia	1968–70	828 (17–45)	0.019215	2.9061	600 (19–47)	0.011529	3.0573
Washington–Oregon	1968–71	656 (18–45)	0.038384	2.7411	682 (24–46)	0.019495	2.9337
Total		4231			3667		

[a] For the formula $W = aL^b$, where W = weight in grams, and L = fork length in centimeters.
[b] N = numbers sampled. Size range (*cm*) in parentheses.

TABLE 2. Length–weight coefficients, sexes combined, and calculated weights (*g*) at selected lengths for Pacific ocean perch, by area.

Area	Source	Coefficients[a]		Calculated weight (*g*) at		
		a	*b*	25 cm	35 cm	45 cm
W Bering Sea	This study	0.025566	2.8305	232	600	1222
E Bering Sea	" "	0.007950	3.1441	198	569	1254
Aleutian Islands	" "	0.037977	2.6929	221	546	1075
Unimak	" "	0.018286	2.9020	208	553	1147
Shumagin Islands	Westrheim (1967)	0.032038	2.72733	208	521	1034
Kodiak	This study	0.013101	3.0109	212	584	1244
	Chikuni (1971)	0.015439	2.9485	204	551	1156
Yakutat	This study	0.014052	2.9997	219	602	1279
SE Alaska	This study	0.016882	2.9429	219	591	1238
	Westrheim (1971)	0.014023	2.98899	211	578	1225
British Columbia	This study	0.010909	3.0660	211	591	1278
	Westrheim and Thomson (1971)	0.0088955	3.13325	213	613	1346
Washington–Oregon	This study	0.023938	2.8746	250	657	1353
	Westrheim (1958)	0.010313	3.08686	213	602	1308

[a] For the formula $W = aL^b$, where W = weight in grams and L = fork length in centimeters.

All data were compiled, and processed by computer, at the Pacific Biological Station. For comparative purposes, processing procedures followed those of Westrheim and Thomson (1971). Regression parameters were obtained by the iterative method rather than the conventional log–log method.

Results — Measurements of 4231 male and 3667 female ocean perch were used in this analysis (Table 1). Most of the data were collected during the third and fourth quarters of the year — only the British Columbia area was sampled in all four quarters. Values of *a*, in the formula $W = aL^b$, for males ranged from 0.014168 (Kodiak) to 0.041569 (Aleutian Islands), and for females, 0.0076028 (E Bering Sea) to 0.054000 (W Bering Sea). Values of *b* for males ranged from 2.6621 (Aleutian Islands) to 2.9881 (Kodiak), and for females, 2.6345 (W Bering) to 3.1694 (E Bering Sea).

Unimak, Kodiak, and Yakutat formulae were tested empirically with length–frequency samples of known weight collected from each of these areas by the Canadian research vessel *G. B. Reed* during 1963–65. The results, listed below, indicate an overall accuracy of –6.7 to +5.8%. Only the Yakutat formula appears to have a bias, which is positive.

		% deviation	
Area	No. of samples	Range	Mean
Unimak	5	–2.0 to +2.5	+0.3
Kodiak	8	–6.7 to +5.8	+1.7
Yakutat	6	+2.4 to +5.6	+4.2

Kodiak, SE Alaska, British Columbia, and Washington–Oregon formulae were tested by comparing calculated weights, at selected lengths, with those of other formulae from the same area (Table 2). The results, listed below, indicate good agreement except for the Washington–Oregon formula.

	% deviation at:		
Area	25 cm	35 cm	45 cm
Kodiak	+3.9	+6.0	+7.6
SE Alaska	+3.8	+2.2	+1.1
British Columbia	–0.9	–3.6	–5.1
Washington–Oregon	+18.8	+10.0	+3.8

The Kodiak formula produced calculated weights consistently larger (3.9–7.6%) than those from Chikuni's (1971) formula. The SE Alaska and British Columbia formulae produced calculated weights quite similar (–5.1 to +3.8%) to those of Westrheim (1971) and Westrheim and Thomson (1971), respectively, whose accuracy had been established, empirically, to be about ±5%. The Washington–Oregon formula produced substantially larger (3.8–18.8%) calculated weights than that of Westrheim (1958), and is suspect since the latter formula produced satisfactory estimates in a catch-sampling study (Westrheim 1967). All of these comparisons would likely yield statistically significant differences. Westrheim and Thomson (1971) found statistical differences (using covariance analysis), by sex, area, and season, for deviations of 2–8%. However, as the absolute accuracy of catch weights or landed weights is probably no better than 5–10%, the conventional statistical tests seem inappropriate.

Among areas, calculated weights at selected lengths were generally maximal at the extreme ends of the study region — Bering Sea and Washington–Oregon (Fig. 1 and Table 2). These interarea differences were most pronounced for 45-cm fish and least so for 25-cm fish. Notably, the Bering Sea fish were appreciably heavier per selected length than those in adjacent areas to the south and east. For example, calculated weights of 45-cm fish were 1222 g in the W Bering area, 1254 g in the E Bering area, and 1075–1147 g in the Aleutian–Unimak region.

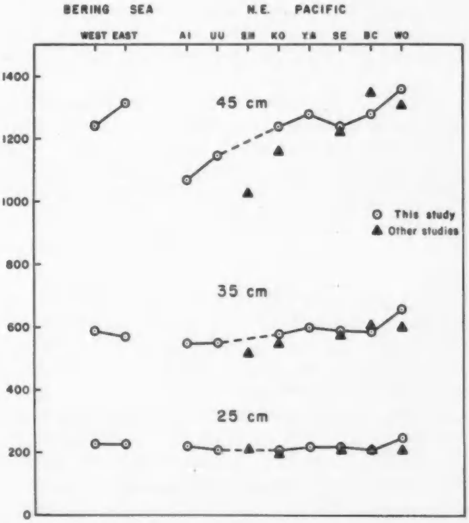

FIG. 1. Calculated weights, by area, of 45-, 35-, and 25-cm Pacific ocean perch (*Sebastes alutus*). Areas: AI = Aleutian Islands; UU = Unalaska–Unimak; SH = Shumagin; KO = Kodiak; YA = Yakutat; SE = SE Alaska; BC = British Columbia; WO = Washington–Oregon.

Discussion — Interarea comparisons of the length–weight relations provided additional evidence of discrete stocks of Pacific ocean perch in the North Pacific Ocean. Calculated weight, by selected length, increased eastward and southward from the Aleutian Islands area to the Washington–Oregon area. These weight differentials suggest there are discrete stocks of Pacific ocean perch along the coast of North America. Other workers have deduced the same situation based on catch records (Fadeev 1968), size composition and dominant year-classes (Westrheim 1970), length–weight and length–girth (Westrheim 1971), fecundity, spawning season, age at maturity, mean length, and mean weight (Snytko 1971a, b), and growth (Westrheim 1973).

Interregional comparisons suggest that the Bering Sea specimens are different from those in adjacent Aleutian and Unimak areas. Calculated weights, at selected lengths, in the Bering Sea region are generally greater. This phenomenon seems to reflect the difference between the two subspecies of Pacific ocean perch proposed by Barsukov (1964) — *Sebastes alutus paucispinosus* (Honshu Island to Southeast Bering Sea) and *S. a. alutus* (Aleutian Islands to California). He noted in his key that body depth at the origin of the ventral fins was generally greater for *S. a. paucispinosus*.

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A Simple Apparatus for Metering Volatile Liquids into Water

PETE E. BENVILLE JR. AND SID KORN

National Marine Fisheries Service
Tiburon Fisheries Laboratory, Tiburon, Calif. 94920, USA

BENVILLE, P. E. JR., AND S. KORN. 1974. A simple apparatus for metering volatile liquids into water. J. Fish. Res. Board Can. 31: 367–368.

A metering device was developed to introduce benzene, toluene, xylene, and 1,2,4 trimethylbenzene vapors into water using air as a carrier gas. Setting the carrier gas flows for the respective aromatics at 10, 25, 120, and 500 cm^3/min for 2 h resulted in concentrations of 8.2, 13.0, 12.0, and 7.2 μl/liter, respectively, in 4 liters of water. The aromatic concentrations were maintained in a static system by bubbling air through the water, and in a continuous flow system by replenishing the water. In static systems the respective aromatic concentrations were maintained for 4 days within the ranges of 13–14, 5.1–7.0, 0.40–0.50, and 0.018–0.028 μl/liter by bubbling the aromatics into the water at 5 cm^3/min and independently aerating the water at 100 cm^3/min. In a 14-day continuous flow system benzene concentrations ranged from 2.1–2.8 μl/liter when benzene was bubbling at 23 cm^3/min and water was flowing at 1.8 liters/min.

BENVILLE, P. E. JR., AND S. KORN. 1974. A simple apparatus for metering volatile liquids into water. J. Fish. Res. Board Can. 31: 367–368.

Nous avons mis au point un compteur pour mesurer les vapeurs de benzène, toluène, xylène et 1,2,4 triméthylbenzène introduites dans l'eau, utilisant l'air comme gaz porteur. Le réglage des débits du gaz porteur, pour les aromatiques respectifs, à 10, 25, 120 et 500 cm^3/min pendant 2 h donne des concentrations de 8.2, 13.0, 12.0 et 7.2 μl/litre, respectivement, dans 4 litres d'eau. Les concentrations d'aromatiques sont maintenues en régime statique par barbotage d'air dans l'eau ou en régime à flot continu par renouvellement de l'eau. En régime statique, les concentrations d'aromatiques respectifs ont été maintenues pendant 4 jours dans les limites de 13–14, 5.1–7.0, 0.40–0.50 et 0.018–0.028 μl/litre en barbotant les aromatiques dans l'eau au taux de 5 cm^3/min et en aérant l'eau indépendamment au taux de 100 cm^3/min. En régime à flot continu pendant 14 jours, les concentrations de benzène ont varié de 2.1 à 2.8 μl/litre avec barbotage de benzène au taux de 23 cm^3/min et débit d'eau de 1.8 litres/min.

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THIS note describes a device that vaporizes liquids, meters their vapors into water, and maintains their concentration in water for extended periods. The liquids that are currently being used in our acute and chronic studies on fish are benzene, toluene, xylene, and 1,2,4, trimethylbenzene. We determined that these aromatics are relatively insoluble in freshwater (1993, 401, 221, and 104 µl/liter, respectively) and volatilize rapidly from water. We found that 46–56% of these aromatics volatilized within 24 h from a 4-liter solution maintained at 20 C. Aerating the solution at 20 cm^3/min increased the loss to 97–100%. Other metering apparatuses (American Public Health Association 1971; Mount and Warner 1965; Mount and Brungs 1967) were not suitable for metering these compounds because of the low solubilities, high volatilities, and high dosages necessary to produce toxic effects in fish. Our system avoids these difficulties by using air as a carrier to introduce the volatile compound into water. Another air source or water flow is used to maintain a stable concentration of the compound in water.

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The metering systems — The static metering system is composed of two independent air sources (Fig. 1). One air source vaporizes the volatile liquid in the gas washing bottle and transports the vapor into the water. The vapor dissolves in the water and accumulates if there is no second air stream until saturation is reached. An accumulation experiment was conducted with four aromatics by aerating each aromatic into 4 liters of water at 20 C, one vapor flow rate being used for each aromatic. The concentrations of these aromatics were determined at three time intervals by extracting a 100-ml water sample twice with 10 ml of TF Freon (trifluorotrichloroethane). An aliquot of the 20-ml extract was injected into a gas chromatograph equipped with a 6-ft column. The column was

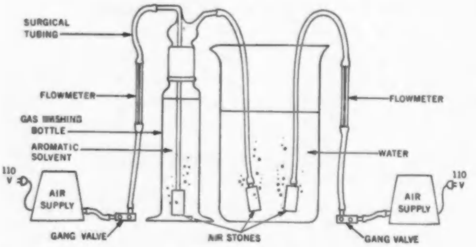

FIG. 1. Components of the static metering system.

packed with 5% Bentone-34 and 10% didecylphthalate on 80/100 mesh chromosorb PAW. The four aromatics accumulated rapidly in water (µl/liter):

Time (h)	0.5	1	2
Benzene (10)[a]	1.4	3.5	8.2
Toluene (25)	3.0	6.2	13
Xylene (120)	3.8	6.6	12
1,2,4 Trimethylbenzene (500)	3.7	5.8	7.2

[a] Vapor flow (cm^3/min).

Low concentrations of the aromatics in water are maintained by utilizing a second air source to limit accumulation of the dissolved vapors in water. At specific vapor and air flow settings an equilibrium is reached between the amounts of vapor dissolving and dissipating from the water. A 4-day equilibrium study was conducted with the four aromatics to determine the daily fluctuations in concentration. The air flows were set at 5 cm^3/min for vaporizing the aromatics and at 100 cm/^{3}min for aerating the water. For water samples taken daily after 24 h the concentrations (µl/liter) were:

Day	1	2	3	4
Benzene	14	13	14	13
Toluene	5.1	7.0	6.7	7.0
Xylene	0.50	0.41	0.43	0.40
1,2,4 Trimethylbenzene	0.028	0.024	0.024	0.018

In a continuous flow system the second air source is replaced by a flowing water source. With a continuous flow system that we had in operation for 2 wk, benzene concentrations were maintained at 2.1–2.8 µl/liter in 65 liters of water at 12 C. The vapor flow was 23 cm^3/min, the water flow 1.8 liters/min.

In both the static and flowing systems the air flow is observed on a flowmeter and controlled by a gas or gang valve. To maintain a constant air flow we tried three different air sources. In order of reliability, these are an air cylinder with a two stage regulator, an oilless air compressor with reservoir, and an aquarium air pump.

We found variations in the dissolved aromatic concentrations between some systems even though the flow rates were identical. Factors that caused the most variation in the concentrations were coarseness of the air stone or fritted disc, volume of the water, and shape of the aquaria. Also, temperature and salinity would be expected to affect the concentrations. Poon (1972) has discussed in depth the various factors influencing bubble aeration. Therefore, each system must be calibrated and furthermore should be monitored periodically as a quality control measure.

Advantages of the technique — Fish undergo many stresses during toxicity experiments that are not necessarily related to the compound being tested. Some of these stresses (such as decreasing oxygen concentrations and increasing carbon dioxide, ammonia, and other volatile wastes) may produce additive effects which bias the results. These stresses are reduced in our technique by aeration.

Some and perhaps most toxicants metered into aquaria are sufficiently insoluble in water to necessitate using a solubilizing agent with the toxicant. The solubilizing agent has a toxic effect on fish that can result in synergistic or antagonistic biases in the toxicity data. Our technique disperses the toxicant into the aquaria without a second compound.

The toxicants are replenished instantaneously in the solution, thereby maintaining a constant toxicant concentration. Any toxicant concentration in water below the saturation level can be achieved by changing one or both of the flow rate ratios, i.e. toxicant aeration to aquarium aeration and toxicant aeration to water flow. Thorough mixing of the toxicant is achieved by aeration. The toxicant is vaporized before it goes into solution, reducing the formation of colloidal particles and precipitates.

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Mercury in Some Canadian Atlantic Coast Fish and Shellfish

H. C. FREEMAN, D. A. HORNE, B. MCTAGUE, AND M. MCMENEMY

Department of the Environment
Fisheries and Marine Service, Halifax Laboratory, Halifax, N.S.

FREEMAN, H. C., D. A. HORNE, B. MCTAGUE, AND M. MCMENEMY. 1974. Mercury in some Canadian Atlantic coast fish and shellfish. J. Fish. Res. Board Can. 31: 369–372.

All species of North Atlantic fishes studied, with the exception of two groups of offshore lobsters, had total mercury levels less than the 0.5 ppm limit allowed for fish of commerce in Canada and the United States. There appeared to be no relationship between mercury levels and the sex and/or weight of fish of any one species.

The first indication that mecury was a threat to public health came from the Japanese mercury poisoning epidemics in the early 1950s (Löfroth 1969; Berglund et al. 1971). This initiated many studies. Apparently increased industrial and agricultural use and the broad dissemination of mercury compounds had caused mercury contamination in fish (Nuorteva 1971).

FREEMAN, H. C., D. A. HORNE, B. MCTAGUE, AND M. MCMENEMY. 1974. Mercury in some Canadian Atlantic coast fish and shellfish. J. Fish. Res. Board Can. 31: 369–372.

Toutes les espèces de l'Atlantique Nord que nous avons examinées, à l'exception de deux groupes de homards du large, ont des niveaux de mercure total inférieurs à la limite de 0.5 ppm permise pour les poissons de commerce au Canada et aux Etats-Unis. Il ne semble pas y avoir, chez les poissons d'aucune espèce, de relation entre le niveau de mercure et le sexe et/ou le poids.

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IN spite of extensive use of mercury and organic mercury compounds there have been no documented cases of mercury poisoning in man from eating fish or shellfish except in the epidemics in Japan where contamination was caused by the emission of mercury by nearby industries. Nevertheless, fishing has been restricted in Sweden and also in North America where the United States and Canada have placed an allowable limit of 0.5 ppm mercury in fish of commerce.

The present study was implemented to determine mercury levels in some of the Atlantic marine species to have a better understanding of mercury contamination in the marine food chain. We thought this information was important to establish a baseline for comparison with possible future changes.

Materials and methods — Most samples were caught in Maritime coastal waters during the summer of 1972. Clams, oysters, quahogs, and mussels were obtained in Malpeque Bay near Ellerslie, P.E.I.; Atlantic salmon, herring, halibut, haddock, hake, cusk, pollock, catfish, lumpfish, menhaden, squid, and rock crabs were caught in the vicinity of Little Harbour, Halifax Co., N.S.; redfish, cod, gaspereau, American plaice, winter flounder, shad, sea raven, and thorny skate were caught off Halifax harbour, mackerel were caught at St. Margaret's Bay, N.S.; red crabs were obtained at La Have Bank, N.S.; silver hake were caught at lat 43°45′40″ N, long 62°43′35″ W; "deep sea" lobsters were caught at sea approximately 100 miles southeast of Shelburne, N.S. and the scallops were caught in Northumberland Strait off Pictou, N.S.

Approximately 25 g of each tissue for total mercury determinations was removed, homogenized, and stored at –25 C prior to analysis.

Total mercury of each fish was determined in duplicate on acid digests of tissue homogenates using a semiautomated flameless atomic absorption method as described by Armstrong and Uthe (1971).

Results and discussion — In comparing the mean total mercury concentration of each species (Table 1) there appears to be no relationship between mercury levels, sex, and/or weight of any one species. With one exception, the tail muscles of the offshore lobsters, all species exhibited total mercury levels below 0.5 ppm.

Comparing the data for Atlantic coast Canadian fish (Table 1) with that obtained by Westöö (1967) for fish caught in the ocean off Scandinavia, in the Baltic, and in Swedish freshwaters, concentration of mercury in the Canadian fish is nearer that

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TABLE 1. Mercury in Atlantic fish and shellfish.

Family	Species	Sex	No. of fish	Avg wt (*g*)	Tissue	ppm Hg range	Mean ± SD[a]
Mytilidae							
mussel	(*Volsella modiolus*)	–	9	41.7	total muscle	0.02–0.05	0.04±0.01
Veneridae							
quahog	(*Venus mercenaria*)	–	10	60.2	" "	<0.005–0.04	<0.02
Myacidae							
clam	(*Mya arenaria*)	–	10	61.4	" "	0.03–0.13	0.05±0.03
Ostreidae							
oyster	(*Crassostrea virginica*)	–	10	24.9	" "	0.06–0.13	0.10±0.02
Pectinidae							
scallop	(*Placopecten magellanicus*)	–	10	–	" "	0.07–0.10	0.09±0.01
Caneridae							
rock crab	(*Cancer irroratus*)	M	10		leg muscle	0.08–0.16	0.12±0.03
Geryonidae							
red crab	(*Geryon quinquedens*)	M	7	873	" "	0.21–0.59	0.38±0.12
		F	3	491	" "	0.23–0.36	0.29±0.05
Homaridae							
lobster	(*Homarus americanus*)	M	8	5526	tail muscle	0.44–1.53	0.73±0.37
"		"	"	"	claw "	0.21–1.13	0.46±0.28
"		F	3	1472	tail "	0.44–0.70	0.61±0.12
"		"	"	"	claw "	0.15–0.34	0.25±0.08
Loliginacea							
squid	(*Loligo forbesi*)	–	8	63	total muscle	0.06–0.11	0.09±0.02
Rajidae							
thorny skate	(*Raja radiata*)	M	3	2745	dorsal muscle	0.13–0.41	0.26±0.14
" "		F	7	2862	" "	0.12–0.22	0.18±0.04
Clupeidae							
gaspereau	(*Alosa pseudoharengus*)	M	6	152	" "	0.05–0.29	0.14±0.08
"		M	4	162	" "	0.08–0.17	0.10±0.03
shad	(*Alosa sapidissima*)	M	9	1072	" "	0.07–0.11	0.09±0.01
"		F	1	962	" "		0.09
menhaden	(*Brevoortia tyrannus*)	M	7	553	" "	0.07–0.11	0.09±0.01
"		F	3	503	" "	0.08–0.11	0.09±0.01
herring	(*Clupea harengus harengus*)	M	10	297	" "	0.06–0.12	0.09±0.02

Salmonidae							
Atlantic salmon	(*Salmo salar*)	M	2	1758	" "	0.10–0.11	0.11±0.01
" "		"	"	"	liver	0.17–0.19	0.18±0.01
" "		"	"	"	kidney	0.14–0.14	0.14
" "		F	8	1644	dorsal muscle	0.07–0.14	0.11±0.02
" "		"	"	"	liver	0.07–0.21	0.15±0.04
" "		"	"	"	kidney	0.04–0.14	0.12±0.03
Gadidae							
cusk	(*Brosme brosme*)	M	6	1604	dorsal muscle	0.09–0.12	0.11±0.01
"		F	4	1246	" "	0.13–0.15	0.14±0.01
cod	(*Gadus morhua*)	M	13	4896	" "	0.14–0.33	0.20±0.05
"		M	6	5429	liver	0.06–0.31	0.13±0.09
"		"	"	"	kidney	0.15–0.24	0.17±0.03
"		F	"	4518	dorsal muscle	0.10–0.34	0.18±0.03
"		"	3	5521	liver	0.04–0.12	0.06±0.03
"		"	"	"	kidney	0.11–0.18	0.13±0.03
haddock	(*Melanogrammus aeglefinus*)	M	10	2397	dorsal muscle	0.06–0.19	0.12±0.04
silver hake	(*Merluccius bilinearis*)	Mixed	10	576	" "	0.04–0.09	0.06±0.02
pollock	(*Pollachius virens*)	M	10	669	" "	0.05–0.13	0.08±0.03
hake	(*Urophycis chuss*)	M	10	4098	" "	0.06–0.19	0.12±0.04
Scombridae							
mackerel	(*Scomber scrombrus*)	M	4	564	" "	0.05–0.16	0.09±0.05
"		F	6	507	" "	<0.005–0.16	<0.08±0.05
Anarhichadidae							
catfish	(*Anarhichas lupus*)	M	2	3057	" "	0.10–0.27	0.19±0.12
"		F	4	3056	" "	0.09–0.31	0.16±0.10
Scorpaenidae							
redfish	(*Sebastes marinus*)	F	10	351	" "	0.11–0.16	0.13±0.02
Cottidae							
sea raven	(*Hemitripterus americanus*)	M	1	1840	" "		0.03
" "		F	9	2745	" "	0.15–0.45	0.30±0.08
Cyclopteridae							
lumpfish	(*Cyclopterus lumpus*)	M	3	1416	" "	0.05–0.06	0.06±0.05
"		F	6	3811	" "	0.04–0.10	0.06±0.02
Pleuronectidae							
American plaice	(*Hippoglossoides platessoides*)	M	2	368	" "	0.12–0.15	0.14±0.02
halibut	(*Hippoglossus hippoglossus*)	F	4	8264	" "	0.16–0.26	0.20±0.03
winter flounder	(*Pseudopleuronectes americanus*)	M	3	557	" "	0.17–0.18	0.17±0.01
" "		F	7	671	" "	0.11–0.20	0.17±0.03

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[a] Standard deviation of the mean.

of the ocean fish caught off Scandinavia. Westöö (1967) found that Baltic sea and Swedish freshwater fish had approximately 19 times as much mercury as ocean fish. Windom et al. (1973) found no difference in mercury levels in offshore and inshore species of fish caught off the coast of South Carolina, Georgia, and Florida. Mercury contamination is not a serious problem in most Canadian Atlantic coast fish.

The total mercury levels of the fish (Table 1) are much lower than that found in North Atlantic swordfish (J. S. Beckett and H. C. Freeman unpublished data) where most of the swordfish, especially the larger ones, had total mercury levels greater than 1 ppm. When considering the low concentration of mercury in the other ocean fish, the high mercury levels in the swordfish may be a natural phenomenon. This is clearly demonstrated by the occurrence of 1–2 ppm methyl mercury in samples of tuna and swordfish that were canned long before the widespread use of mercury by industry (Wood 1972).

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A Method of Measuring Bacterial Growth in Aquatic Environments Using Dialysis Culture

Russell C. Baskett[1] and William J. Lulves

Department of Microbiology
The University of Missouri School of Medicine, Columbia, Mo. 65201, USA

Baskett, R. C., and W. J. Lulves. 1974. A method of measuring bacterial growth in aquatic environments using dialysis culture. J. Fish. Res. Board Can. 31: 372–374.

An inexpensive, easy-to-use method was developed for studying microbial growth and behavior in situ. Dialysis tubing suspended from a styrofoam flotation ring was filled with sterile distilled water, placed in a farm pond, and inoculated with *Brevibacterium* sp. The viable population within the tubing increased significantly within 96 h, indicating that nutrients in the pond water necessary for growth and multiplication of *Brevibacterium* sp. diffused through the dialysis membrane.

Baskett, R. C., and W. J. Lulves. 1974. A method of measuring bacterial growth in aquatic environments using dialysis culture. J. Fish. Res. Board Can. 31: 372–374.

On a développé une méthode d'emploi facile et peu dispendieuse pour étudier la croissance et le comportement microbiens in situ. Une cellule de dialyse, suspendue sur un anneau de flottaison en polystyrène, est remplie d'eau distillée stérile, placée dans un étang de ferme et reçoit une inoculation de *Brevibacterium*. La population viable dans la cellule augmente de façon significative sur une période de 96 h, ce qui indique que les substances nutritives de l'eau de l'étang, nécessaires à la croissance et à la multiplication de *Brevibacterium*, se diffusent à travers la membrane de dialyse.

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[1] Present address: Department of Microbiology, Texas Tech. University School of Medicine, Lubbock, Tex. 79409, USA.

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ALTHOUGH the merits of dialysis culture and its applications to microbial growth have been recently reviewed (Schultz and Gerhardt 1969), only a few investigators have applied this technique to in situ aquatic studies (Trainor 1965; Hendricks and Morrison 1967; Jensen et al. 1972). Only one group of these investigators (Hendricks and Morrison 1967) utilized bacterial cultures, and their technique did not permit daily sampling from the same dialysis bag over an extended period of time. This report describes a simple dialysis apparatus suitable for culturing bacteria that can be left in a lake or pond for long periods of time and allows for daily sampling without the removal and disruption of the dialysis bags.

The apparatus (Fig. 1) consists of a styrofoam flotation ring connected by threaded brass rods to a bottom ring of heavy rubber garden hose. Twenty-six-centimeter lengths of 48-mm dialysis bags, boiled for 1 h in distilled water to remove residual sulfur, are plugged at one end with solid no. 11 neoprene stoppers and at the other end with one-hole neoprene stoppers fitted with glass tubes and suspended between the rings. After boiling, the dialysis bagging is never allowed to dry out since it becomes brittle upon drying. The glass tubing is plugged with rubber stoppers and covered with thin-walled plastic centrifuge tubes to prevent contamination of the bags. The bag assemblies are sterilized by autoclaving at 121 C for 15 min before being connected to the rings. In a typical experiment, the sterile bag assemblies are connected to the suspending apparatus and filled with 350 ml sterile distilled water. The entire apparatus is then suspended in a farm pond and held in place with a mushroom anchor. The bags are left undisturbed for 48 h to allow for equilibration between the pond water and the contents of the bags. Following the equilibration period, the bags are inoculated through the glass tubing with a washed suspension of the organism being studied. At predetermined time intervals, the contents of the bags are mixed with a 10-ml pipette and aliquots removed for plating on predried tryptone glucose yeast extract agar plates (Hentges 1962).

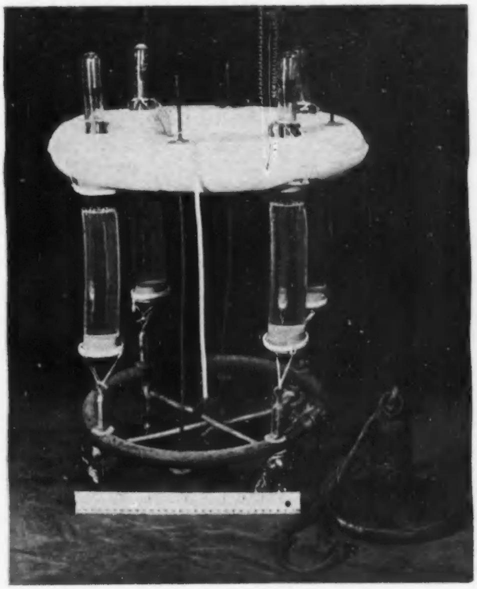

FIG. 1. Dialysis culture apparatus.

To test the apparatus, experiments were conducted in the field using an unidentified species of *Brevibacterium* that was originally isolated from the farm pond. As a control, round-bottomed flasks containing 350 ml sterile distilled water were also suspended in the pond, left undisturbed for 48 h, and inoculated at the same time as the bags. The viable populations in both the bags and flasks were determined, as described above, at the time of inoculation and after incubation for 24, 48, 72, and 96 h. The viable cells per milliliter in the bags and flasks in a representative experiment were:

Hours after inoculation	Dialysis bags	Flasks
0	7.8×10^4	7.5×10^4
24	2.6×10^5	4.0×10^2
48	8.2×10^5	0
72	1.0×10^6	0
96	1.2×10^6	0

Growth was evident in the dialysis bags during the 96-h incubation period, with the viable population increasing from 7.8×10^4 to 1.2×10^6 cells per milliliter. In the control flasks, *Brevibacterium* sp. did not multiply but died off rapidly and was undetectable by our plating procedure after 48 h of incubation.

These results indicate that the nutrients requiree for *Brevibacterium* sp. multiplication can diffusd through the dialysis membranes in quantities sufficient to support growth. Although measurements were not made to determine equilibrium concentrations of nutrients, comparative studies using sterile pond water and sterile distilled water demonstrated that similar growth occurred in the two waters after the 48-h equilibration period.

These data demonstrated that dialysis culture is an effective tool for the assessment of bacterial growth in an aquatic environment. This technique is versatile and has many applications to aquatic microbiology in either its present or modified form.

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Pautov, G. B. 1972. Some characteristic features of the biology of Pacific Ocean perch (*Sebastodes alutus* Gilbert) in the Bering Sea. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (TINRO) 81: 91–117. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2828, 1973) (1)

Matsuo, N. 1972. The reaction between nitrogen compounds and autoxidized fatty acid ester. Seikei Daigaku Kogakubu Kogaku-Hokoku 14: 1107–1116. (Transl. from Japanese by Fish. Res. Board Can. Transl. Ser. No. 2829, 1973) (8)

Markovtsev, V. G. 1972. Feeding and food relationships of young sockeye and three-spine stickleback in Lake Dalnee. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (TINRO) 82: 227–233. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2830, 1973) (1)

Kracht, D. 1972. Experimental biology. Application of winter and summer conditions, removal of the ocular peduncles, and action of an ecdysterone on the adult female crayfish *Orconectes limosus* R., during the anecdysis period: consequences on egg laying and molting. C. R. Acad. Sci. Paris (Sér. D) 275: 1677–1680. (Transl. from French by Fish. Res. Board Can. Transl. Ser. No. 2831, 1973) (6)

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Charmantier, G., and J.-P. Trilles. 1973. Invertebrate physiology. Reestablishment of the molting phenomena by the injection of ecdysterone to pubescent adult males of *Sphaeroma serratum* (Crustace, Isopode) C.R. Acad. Sci. Paris (Sér. D) 276: 2561–2564. (Transl. from French by Fish Res. Board Can. Transl. Ser. No. 2833, 1973) (6)

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Timm, T. E. 1967. The life cycle of some Oligochaeta. Tr. Karel. Odt. GosNIORKh 5: 202–204. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2838, 1973) (4)

Polyanskaya, A. I., and V. A. Amineva. 1971. Morphology of the brain of the freshwater eel (*Anguilla anguilla* L.). Atl. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (AtlantNIRO) (Voprosy povedeniya ryb.) p. 145–148. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2839, 1973) (6)

Zaferman, M. L. 1972. Observations on capelin in the area of the Hope Island. Mater. Rybn. Khoz. Issled. Servernogo Basseina 19: 93–100. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2840, 1973) (9)

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Stang-Voss, C. 1971. Studies on the ultrastructure of invertebrate hemocytes V. On the hemocytes of *Astacus astacus* (L.) (Crustacea). Z. Zellforsch. 122: 68–75. (Transl. from German by Fish. Res. Board Can. Transl. Ser. No. 2842, 1973) (8)

Vadze, D. R. 1967. Comparative description of the macrozoobenthos in Ilzes-Geranimovas, Rushonu, Felmanyu, and Pitelyu lakes. Tr. Karel. Otd. GosNIORKh 5: 192–195. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2843, 1973) (4)

Bukhanevich, I. B. 1971. On the interaction of recruitment, growth and mortality in fish (Biological principles and ways of increasing the efficiency of natural reproduction and rearing of valuable commercial fishes). Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 86: 180–189. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2844, 1973) (7) (9) (6)

Klyavsons, Y. A. 1972. Significance of separate blood serum protein fractions in the regulation of water-salt metabolism in salmonids. (Problems of fish physiology.) Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 85: 103–106. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2845, 1973) (7) (9)

Fomichev, A. V. 1971. On the recurrence of conditions for the coastal upwelling in the zones of eastern boundary currents. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 86: 19–25. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2846, 1973) (9)

Fontaine, M. 1972. Endocrine glands and various forms of fish behaviour. Tr. Tsentr. Lab. Vosproizvodstvu Rybn. Zapasov Glavrybvoda MRKh SSSR: 158–166. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2847, 1973) (2)

Nikolaev, I. I., I. N. Andronikova, and E. A. Shushkina. 1967. On the vertical distribution of zooplankton (excluding protozoans) in the deep-water region of Lake Ladoga. Tr. Karel. Otd. GosNIORKh 5: 126–128. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2848, 1973) (4)

Persov, G. M. 1966. Early stages of gametogenesis in diadromous salmon. In symposium "Vosproizvodstvo i akklimatizatsiya lososevykh v Barentsovom: Balans v moryakh." Tr. Kol. fil. Murmansk. Morsk. in-ta 12: 7–44. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2849, 1973) (1)

Bubnova, N. P. 1971. The size-weight characteristics of *Macoma baltica* (L.) in Kandalaksha Bay on the White Sea. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. (VNIRO) 86:

67–69. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2850, 1973) (9)

Barsuk, L. N. 1972. Biochemical study of Far Eastern salmon during spawning migration. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. (TINRO) 79: 127–133. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2851, 1973) (8) (9)

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Bobrov, Yu. A. 1970. The dependence of the rate of photosynthesis at various depths on temperature and light. Vestn. Mosk. Univ. Sec. VI Biol. Pochvored 25: 91–93. (Transl. from Russian by Fish. Res. Board Can. Transl. Ser. No. 2853, 1973) (7)

Additional Publications

The Service also publishes a series of *Bulletins*, each on a specific topic. These are for sale by Information Canada, Ottawa, and remittances must be in advance, payable in Canadian funds to the order of the Receiver General of Canada. *Bulletins* are also available from local booksellers and Information Canada bookshops throughout Canada.

The *Annual Report* of the Board and the biennial *Review* of investigations are available free, on request. All publications may be referred to at establishments located at: Ottawa; Nanaimo, Vancouver, and West Vancouver, B.C.; Winnipeg, Man.; Ste. Anne de Bellevue, Que.; St. Andrews, N.B.; Halifax and Dartmouth, N.S.; and St. John's, Nfld.

Le Service publie également une série de *Bulletins*, chacun traitant sur un sujet spécifique. Les publications de l'ORP sont vendues par Information Canada à Ottawa. Les remises, payables d'avance en monnaie canadienne, doivent être établies à l'ordre du Receveur général du Canada. Les *Bulletins* sont aussi en vente chez votre libraire et dans les librairies d'Information Canada.

Vous pouvez obtenir le Rapport Annuel et la Revue biennale gratuitement. On peut consulter ces ouvrages aux établissements situés à Ottawa (Ont.) à Nanaïmo, à Vancouver, et à Vancouver Ouest (C.-B.), à Winnipeg (Man.), à Ste-Anne-de-Bellevue (P.Q.), à St-Andrews (N.-B.), à Halifax et à Dartmouth (N.-E.), et à St-Jean (T.-N.).

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Guide to Authors

A more detailed guide on preparation of manuscripts from theses is available from the Office of the Editor.

EDITORIAL PRACTICES

The *Style Manual for Biological Journals* (3rd ed. American Institute of Biological Sciences, 3900 Wisconsin Ave. NW., Washington, D.C.) is used as the authority in matters of form. The standards for spelling are: *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Third Edition, 1970), Special Publication No. 6 of the American Fisheries Society.

Notes are distinguished from *papers* on the basis of scope or completeness, rather than quality, of the research. They may be on problems with narrow, readily defined limits; on work that is largely confirmatory; on fishing gear or methods, or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued; or on preliminary findings that warrant publication before problems are resolved. They may be organized with as much flexibility as papers except that they may have no centered headings. They should take no more than four pages in the *Journal*.

Series titles should be avoided. An *abstract* is required. Authors are encouraged to submit abstracts in both English and French; those submitted in one language only are translated by the *Journal*.

Line drawings are preferably made with black india ink on white drawing or tracing paper or on coordinate paper with blue grids. All lines, symbols, letters, and numerals must be neat, and at least 1 mm high when the illustration is reduced to the appropriate size. Drawings should be grouped to facilitate comparisons. Originals must be submitted and should be less than 50 cm in the greater dimension for full-page illustrations, and proportionately smaller for those taking less than a page. Drawings must not be rolled for mailing.

Photographs should be printed on glossy paper with a wide range in tone. They should be cropped, squared, and mounted on white cardboard, with no spaces between those arranged in groups.

Galley proof is sent to the author, and he is responsible for detecting errors in printing as well as in content.

Fifty *reprints*, without covers, are supplied free. Additional copies may be ordered when the galley proof is returned. A charge of $30.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

CHECKLIST ON MANUSCRIPTS

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the biology?

Would any of the text be clearer if condensed? Are summary statements given at the beginnings of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data?

Are generalizations on the *results* adequate? Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

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Guide des Auteurs

On peut se procurer au bureau du Directeur de la publication un guide plus détaillé pour la préparation de manuscrits à partir de thèses.

DISPOSITIONS GÉNÉRALES

Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Les *notes* se distinguent des *articles* par la portée et le degré d'achèvement, plutôt que par la qualité des recherches. Les notes peuvent traiter de problèmes à portée restreinte et facilement définissables; de travaux qui en corroborent d'autres; d'engins et de méthodes de pêche, ou de techniques de recherche; de découvertes dérivées d'une recherche de plus grande envergure; de progrès accomplis dans l'exécution de projets abandonnés; enfin, de résultats préliminaires assez importants pour en justifier la publication avant la solution complète du problème. L'agencement des notes peut être aussi flexible que celui des articles, sauf qu'elles ne doivent pas avoir d'en-têtes de paragraphes centrés. La longueur ne doit pas dépasser quatre pages.

On doit en général éviter les *titres en séries*. L'auteur doit fournir un *résumé*. Si possible, le résumé devra être produit en anglais et en français; le *Journal* se charge de la traduction des résumés soumis en une seule langue.

Les *dessins au trait* doivent être éxécutés de préférence à l'encre de Chine sur papier à dessin blanc, sur papier à calquer ou sur papier quadrillé bleu. Lignes, symboles, lettres et chiffres doivent être soignés et mesurer au moins 1 mm de hauteur lorsque la figure est réduite à la dimension voulue. On groupera les dessins de façon à faciliter les comparaisons. Les dessins originaux doivent accompagner le manuscrit, et ne doivent pas dépasser 50 cm dans le sens le plus long s'ils représentent une figure devant couvrir une page entière; ils seront proportionnellement plus petits pour des figures de moins d'une page. Les dessins doivent être postés à plat.

Les épreuves de *photographies* doivent être tirées sur papier glacé à gamme de ton étendue. Elles doivent être coupées, dressées et montées sur carton blanc, sans laisser d'espace entre celles qui sont disposées par groupes.

Les *épreuves en placards* sont adressées à l'auteur et il lui incombe de corriger toute erreur d'impression ou de contenu.

Cinquante *tirés à part*, sans couverture, sont fournis gratuitement. L'auteur peut profiter du renvoi des épreuves en placards pour commander des tirés à part supplémentaires. Les frais sont de $30.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

LISTE DE CONTRÔLES POUR MANUSCRITS

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphes sont-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

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Guide for Typists Preparing Copy

Read "Guide to Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize only the first word and proper names and adjectives. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and another clear copy to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).
Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send the *original* and two clear copies of each illustration with the manuscript. At the lower left of each figure and copy, give the author's name and the figure number. Also, type each caption with its figure for identification. For photographs, type this information on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter $\underline{l}$ and the numeral *one*, and between the capital letter $\overline{\underline{O}}$ and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

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Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21.5 × 28 cm (8.5 × 11 pouces), laissant toujours une marge d'au moins 2.5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les minuscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, le nom et l'affiliation de ou des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, et y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et une seconde copie suffisamment claire au bureau du Directeur de la publication.

Tableaux: Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C).
Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*.

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par des minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Expédiez avec le manuscrit le *dessin original* et deux copies propres de chaque figure. Au coin inférieur gauche de chaque original et copie, inscrivez le nom de l'auteur et le numéro de la figure. De plus, annexez à chaque figure la légende qui lui est propre, pour fin d'identification. Dans le cas de photographies, dactylographiez l'information sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre $\underline{l}$ et le chiffre *un*, et entre la majuscule $\underline{O}$ et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le Journal (voir Appendice E). Les noms de revues sont abrégés suivant les *Biological Abstracts;* en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

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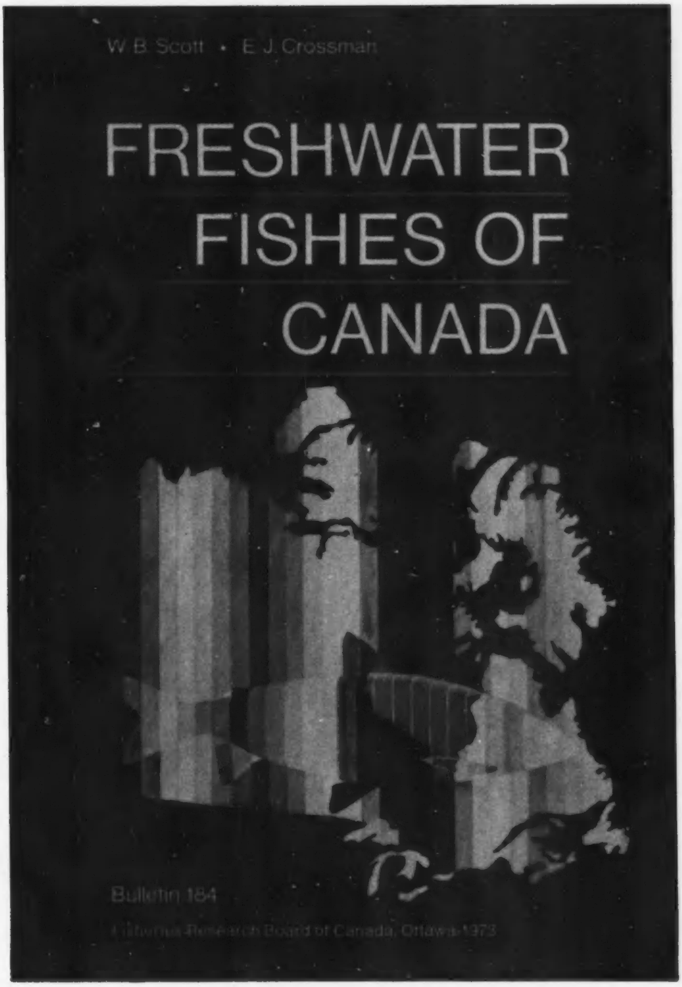
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